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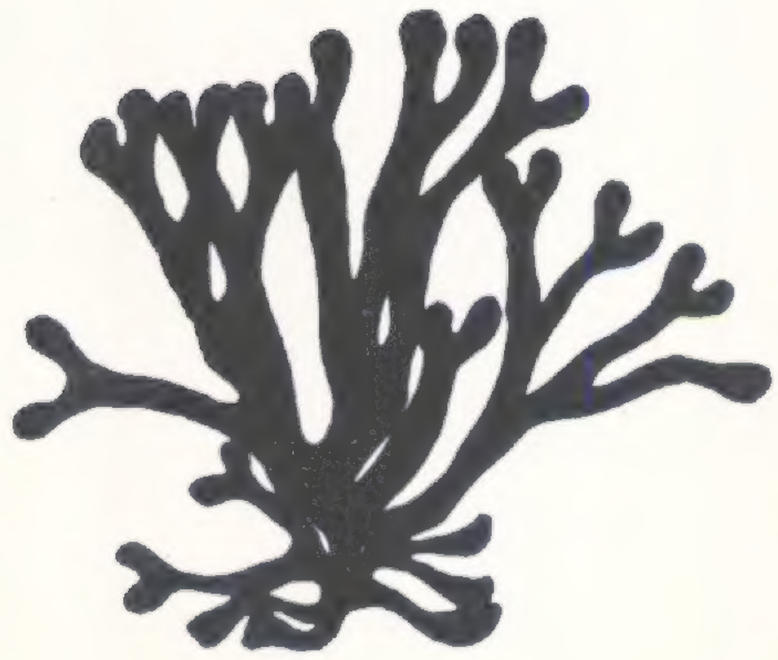
No. 12 April, 1977 Harvard University, Cambridge, Massachusetts

Gayle I. Hansen | Cirrulicarpus Carolinensis, A New Species in the Kallymeniaceae (Rhodophyta)

A Comparison of the Species of Cirrulicarpus (Kallymeniaceae, Rhodophyta)

Monte G. Manuel | Studies in Cryphaeaceae III. Sphaerotheciella Fleisch. New to the Americas



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CIRRULICARPUS CAROLINENSIS, A NEW SPECIES IN THE KALLYMENIACEAE (RHODOPHYTA)

GAYLE I. HANSEN[1]

ABSTRACT

Cirrulicarpus carolinensis sp. nov. is a cartilaginous, complanate, subdichotomously branched, red alga which inhabits the submerged rocky reefs off the North Carolina coast. The plant is perennial and grows by means of a marginal, surface meristem. In section, the blades consist of a medulla of primary stellate and secondary filiform cells and a cortex of large, subglobose inner cells that grade into smaller, nearly globose outer cells. The carpogonial branch apparatus consists of one or two carpogonial branches of three cells and occasionally up to two subsidiary cells borne on a large, lobed supporting cell. Carposporophyte development is distinctive in that the gonimoblast filaments appear to form from vegetative instead of reproductive cells. The life history consists of an alternation of gametophyte and carposporophyte generations.

INTRODUCTION

A new species of *Cirrulicarpus* was found growing in crevices of the rocky reefs off the New River Inlet in North Carolina. In habit the alga resembles *Cryptonemia crenulata* (J. Ag.) J. Ag., a species to which it has been incorrectly referred in earlier papers (Hoyt, 1920; Pearse and Williams, 1951). However, unlike *Cryptonemia*, the new alga has carpogonial branches of three cells borne on a large, lobed supporting cell and very large cystocarps. It is a member of the family Kallymeniaceae and most closely resembles other species of the genus *Cirrulicarpus*, a genus that has not previously been reported from the Atlantic Ocean. A detailed examination of the North Carolina species was undertaken in order to confirm its taxonomic affinities and to understand its biology. The new name *Cirrulicarpus carolinensis* is proposed.

Cirrulicarpus carolinensis Hansen, sp. nov.

Plantae perennes, caespitosae, ad 16 cm altae. Laminae juniores obovoideae integrae, maturae subdichotome ramosae ramis inferis anguste cuneatis, ramis superis obovoideis lobatis. Thallus ex cellulis corticeis parvis (4–8 μm lat.), ex cellulis subcorticeis majoribus (12–40 μm lat.), et medulla cellularum stellatarum primariarum, secundariarum filiformium sonstans. Dioeciae. Plantae femineae fasciculis ramulorum carpogonialium praeditae; omnis fasciculus ex 1 vel 2 ramulis tricellularibus carpogonalibus et 0–2 cellulis subsidiariis e cellula magna exorientibus constans. Carposporophyta laxa; filamenta gonimoblastorum ex filamentis cellulorum brevium constantia; filamenta e cellulis vegetativis exorientia, in cellulis vegetativas panetrantia, et cum cellulis per foveas conjugantia. Cystocarpi non ostiolati, magni (ad 3 mm lat.), fasciculati in superficie frondis, in aetate provecta verrucosi. Plantae masculinae soros sperma-

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tangiorum in pagina thalli irregulatin dispersos efferentes. Spermatangia ex cellulis elongatis vallum supra corticum facientibus evoluta. Tetrasporangia ignota.

TYPE. **North Carolina. Onslow County:** ca. 3.2 km east of New River Inlet at Mile Hammock Rock, depth ca. 5 m, Hansen, 10 October, 1974. HOLOTYPE: NCU. Isotypes to be distributed to: AHFH,BM,DUKE,FH,LD,MEL,PC,UC,WTU, herb. C. Schneider (Trinity College, Connecticut), herb. T. Masaki (Hokkaido University, Japan).

Plants caespitose. Blades entire and obovoid when young, branching subdichotomous when mature; lower branches narrowly cuneate and upper branches obovoid-lobed. Perennial, reaching 16 cm in height. Thallus composed of small cortical cells (4–8 μm in diameter), larger subcortical cells (12–40 μm in diameter), and a medulla of primary stellate and secondary filiform cells. Dioecious. In female plants, the carpogonial branch systems consisting of one or two three-celled carpogonial branches and zero to two subsidiary cells on a large supporting cell. Carposporophytes diffuse; gonimoblast filaments consisting of short-celled filaments which originate from, form pit connections with, and penetrate vegetative cells. Cystocarps non-ostiolate, large (to 3 mm in diameter), arranged in clusters on the upper surfaces of the fronds, and becoming verrucose when old. In male plants spermatangial sori scattered irregularly over the thallus surface. Elongate spermatangial mother cells forming a palisade-like layer above the cortex. Tetrasporangial plants unknown.

Material and Methods. Collections of *Cirrulicarpus carolinensis* were made about every other month over a three year period from 1972 to 1974. Drift material was collected from the south side of the New River Inlet, North Carolina, and attached material was collected by SCUBA from Mile Hammock Rock, a submerged reef located near the Inlet.

Freshly collected material was preserved in 5% formalin in seawater or Carnoy's fixative containing chloroform (Johansen, 1940). The material was prepared for staining by the following methods: (1) hand sectioning with a razor blade; (2) sectioning with a freezing microtome; (3) squashing small pieces under a coverslip; or (4) peeling the upper and lower cortex of the thallus apart with fine needles and placing the inner faces of the cortex upwards on a slide. Material fixed in formalin required no presoftening in alkali (Norris, 1957) or acid (Papenfuss, 1937) before squashing or peeling. These preparations were stained with 1% aniline blue according to the procedure of Papenfuss (1937), except that a 5% hydrochloric acid solution was used to bind the stain. The material was then mounted in Karo syrup containing phenol (Womersley and Norris, 1971).

A 35 mm Nikon camera attached to either a Wild M-5 dissecting microscope or a Zeiss RA light microscope was used for microphotography, and a Pentax Spotmatic camera was used for macrophotography.

Habitat. *Cirrulicarpus carolinensis* inhabits a submerged rocky outcrop located about 3.2 km east of the New River Inlet in North Carolina. This site, called Mile Hammock Rock by local fishermen, appears to be a part of the "Black Rock" reefs studied by Pearse and Williams (1951). These reefs are an outcropping of Lower Miocene Trent Marl. Covered with algae, the rocks attract the blackfish, *Centropristes striates* (L.).

Mile Hammock Rock rises abruptly from the sandy sea floor off the Inlet to about 4.0 m below the surface. The rocks are traversed by many deep, narrow fissures, and are undercut with shallow caves. *Cirrulicarpus* grows in irregularly scattered clumps along the vertical surfaces of the sheltered and shaded walls of the fissures. The fronds are frequently found attached to sea squirts, but growth on the porous rock alone is also quite common. The alga grows at a depth of from 4.5 to 9.0 m below the surface and is perennial. Juvenile plants are seen infrequently throughout the year and are never found in abundance in any particular season. Based on bimonthly observations, the major growing season for *C. carolinensis* appears to be from late spring to late fall. Growth is arrested in the winter. During the summer, *C. carolinensis* dominates the red algal flora at Mile Hammock Rock because most other species have died back to their holdfasts. The fall and spring blooms grade into one another over the winter, and during this time *C. carolinensis* is a minor component of the flora.

Vegetative Structure. Young thalli of *Cirrulicarpus carolinensis* are light pink, cartilaginous, complanate, and obovate with margins that are entire and somewhat undulate (Fig. 1). The blades are attached to the substratum by a short terete stipe and a small discoid holdfast. As the fronds grow, they branch subdichotomously (Fig. 2). As many as ten

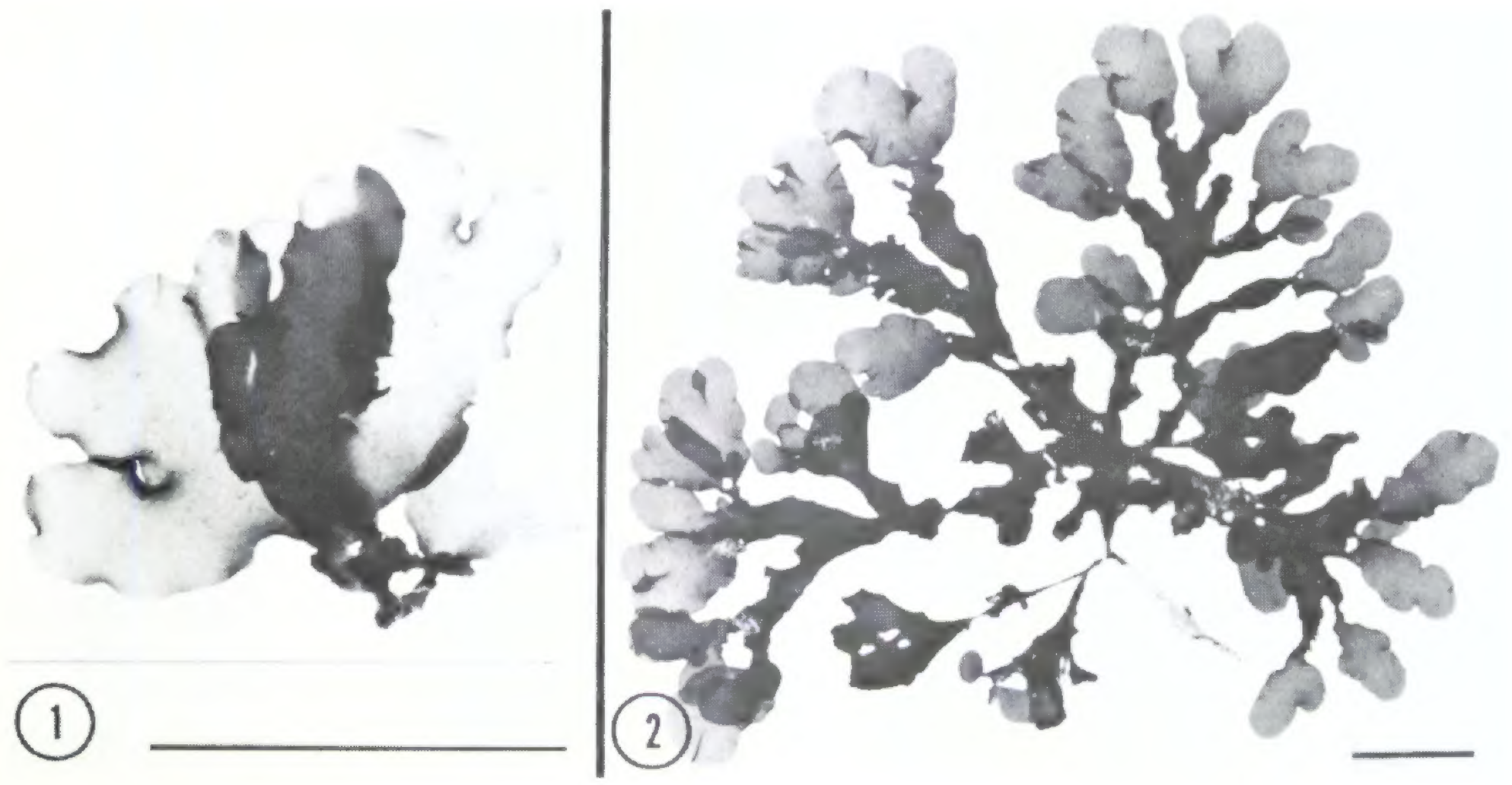


FIG. 1, 2. Young and mature plants of *Cirrulicarpus carolinensis*. Notice the thinner, more transparent quality of the current year's growth; scale, 3 cm.

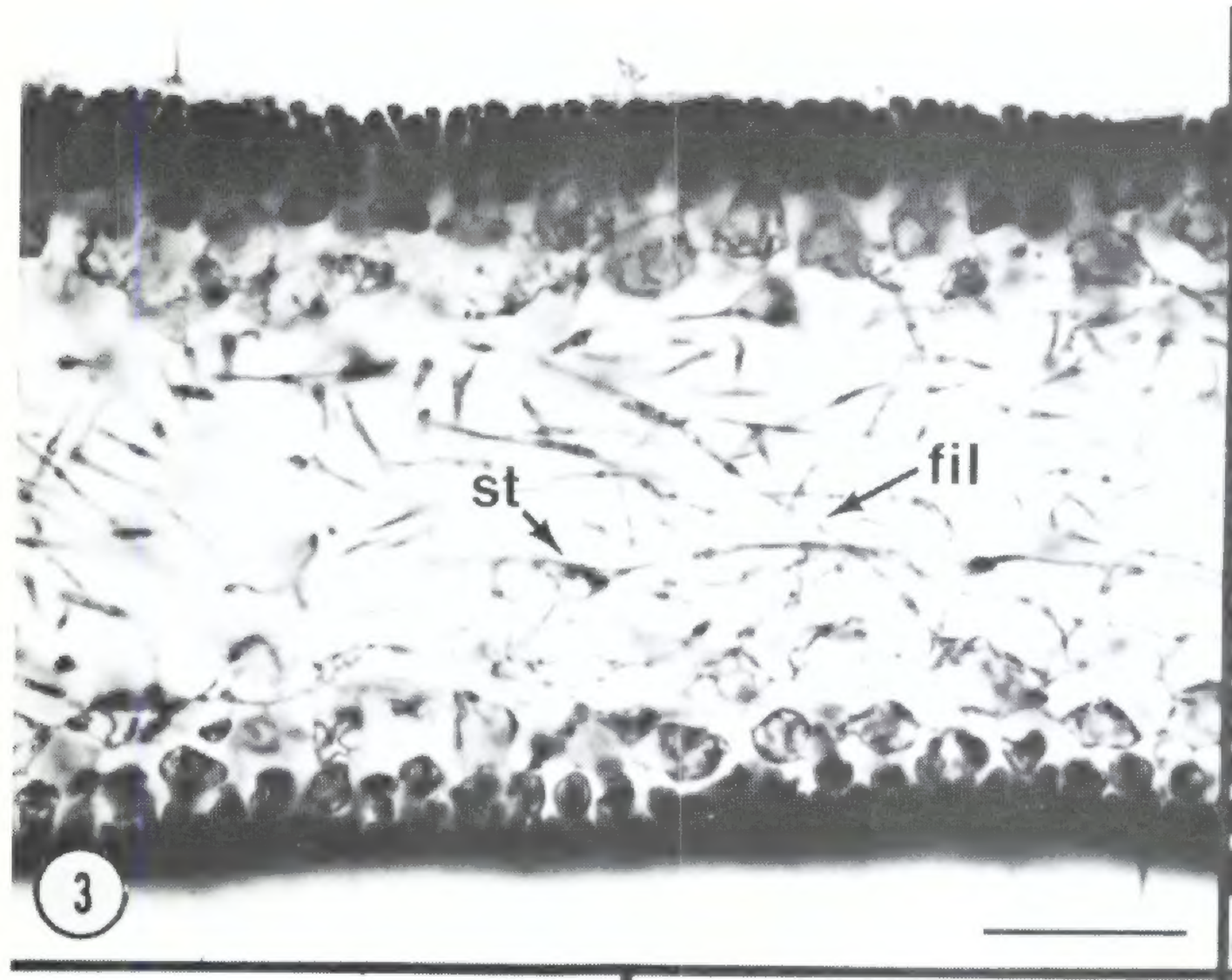
dichotomies were counted in mature plants 16 cm in height. Dichotomies in the older portions of the plant are acute; those near the apex are somewhat rounded. The thallus is broadest near the rounded tips of the ultimate branches and may reach a width of 2 cm. Mature plants are widely foliose and exceedingly undulate and appear in habit like tufts of crowded ruffles.

The alga is perennial and, on the basis of morphological observations, appears to live for from two to four years. During the winter the fronds deepen in color, thicken, and become lacerated and worn. At this stage the plants are often narrowly cuneate in shape. In the spring new growth occurs by a regeneration of the meristematic margins of the blade in certain areas near the apex. These areas are sometimes so narrow that the new bladelets appear attached to the parent plant by a stipe-like region. The bladelets are obovate-lobed like young blades and appear thinner and lighter in color than older parts of the thallus. By these characteristics, the beginning and end of each year's growth can easily be distinguished.

Cross sections of the mature blade show that it is composed of a one- or two-layered outer cortex of small subglobose cells about 4–8 μm in diameter, a subcortex of one or two layers of larger subglobose cells, 12–40 μm in diameter, and a medulla consisting of interlacing stellate and filiform cells (Fig. 3). The stellate cells constitute the primary medulla; the filiform cells are derived secondarily.

In the blade, the primary meristematic areas are located along the margins. The margin at the apex is more active meristematically than the lateral margins where only limited or regenerative growth occurs. In the meristems, growth is initiated through the division of surface cells. Each surface cell may cut off from one to three daughter cells. The first two cells are cut off anticlinally or obliquely, and the last one is cut off apically from the parent cell (Fig. 5). In surface view, these cells appear in groups of one to three (Fig. 4). These groups consist of the parent cell alone, the parent cell in combination with its oblique daughter cells, or the daughter cells alone. As new cells are produced at the meristem, each previous generation of cells is displaced beneath the surface, creating a series of dichotomously or trichotomously branched filaments below the meristem (Fig. 7). Cells of the upper two layers of these filaments are undifferentiated. In the third and fourth layers, the cells begin to form secondary pit connections with neighboring filaments (Fig. 6, 7) but retain their globose, meristematic shape. At this stage, the cells

FIG. 3–10. Anatomy of the blade.—3, cross section showing medullary region containing both filiform (fil) and stellate (st) cells; scale, 50 μm.—4, surface view near the meristematic margin; scale, 20 μm.—5, oblique and periclinal divisions of the terminal meristematic cells; scale, 20 μm.—6, peel preparation of a young cortical region showing the small cells (arrows) involved in the formation of secondary pit connections; scale, 20 μm.—7, peridermal section through the growing tip; scale, 20 μm.—8, section showing the origin of a filiform medullary cell from the subcortex; scale, 30 μm.—9, peel preparation of subcortical cells; scale, 20 μm.—10, squash preparation of stellate cells; scale, 20 μm.



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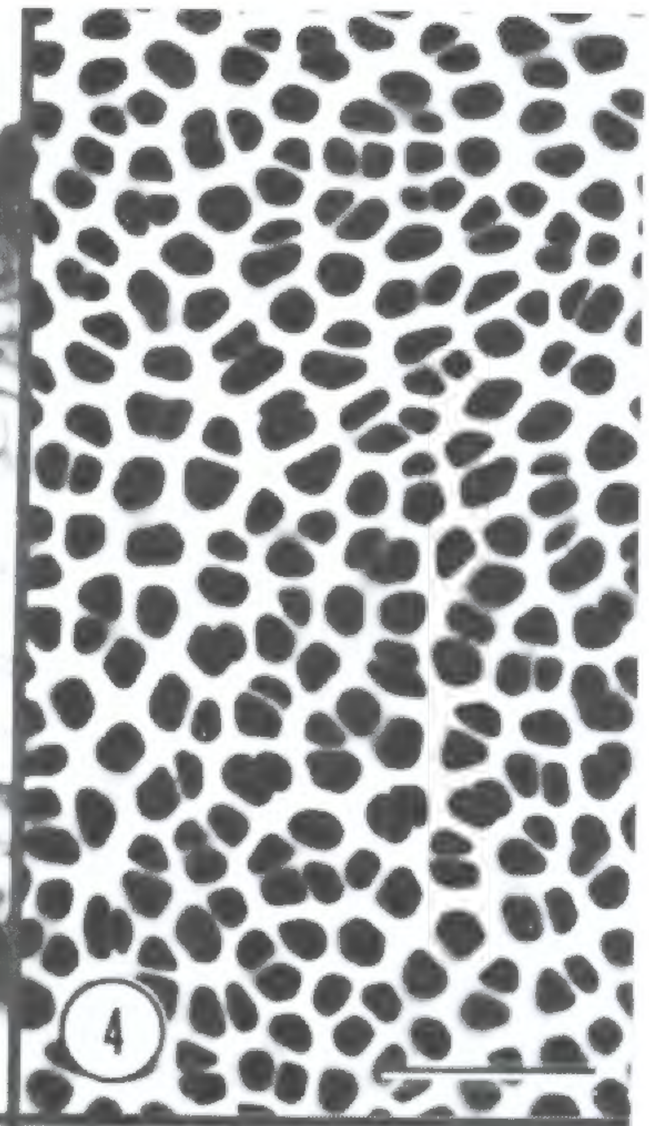

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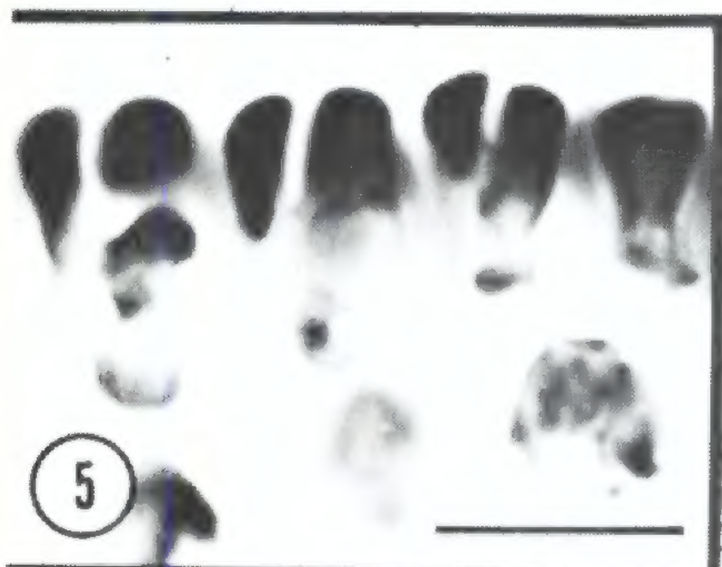

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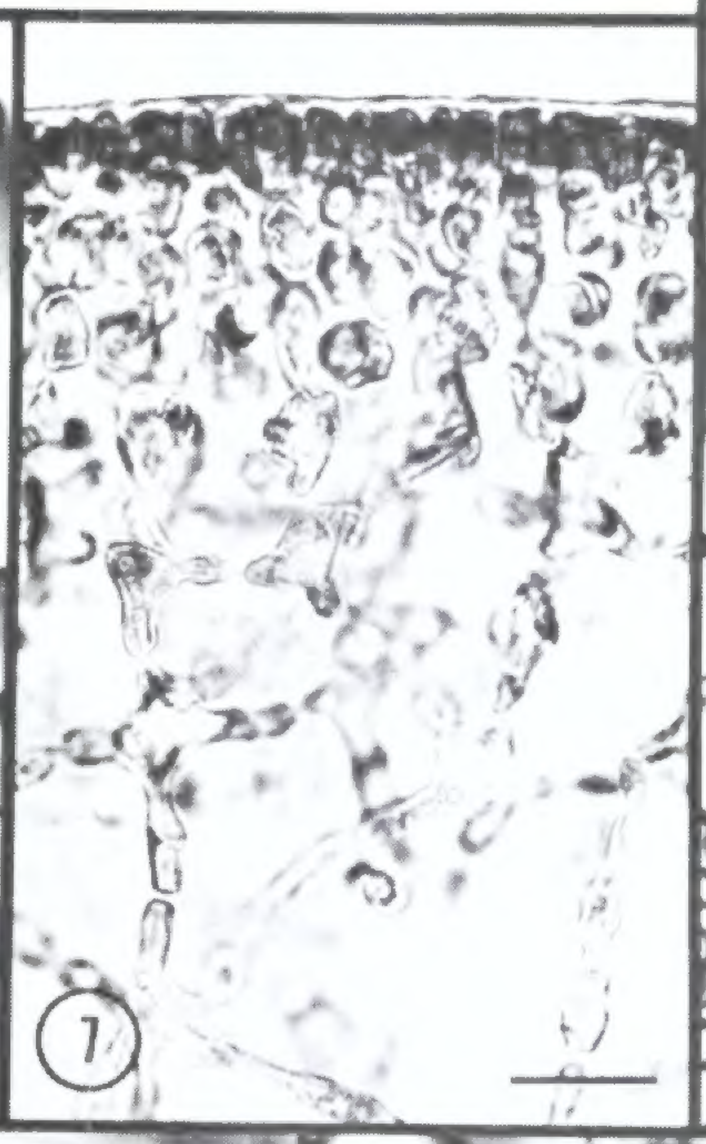

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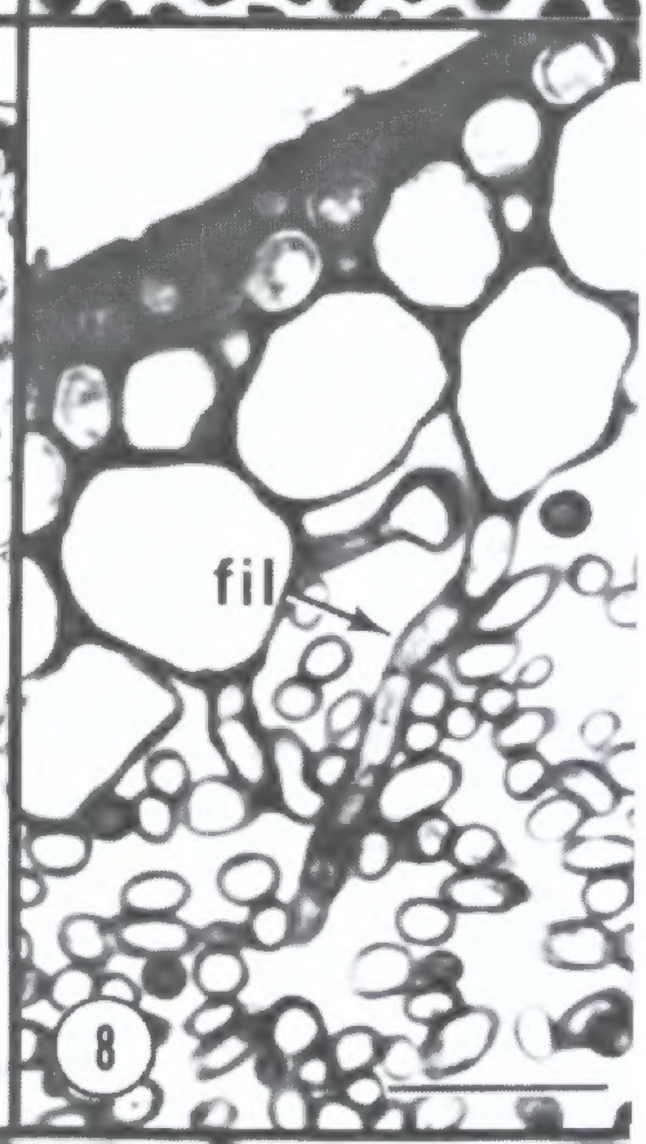

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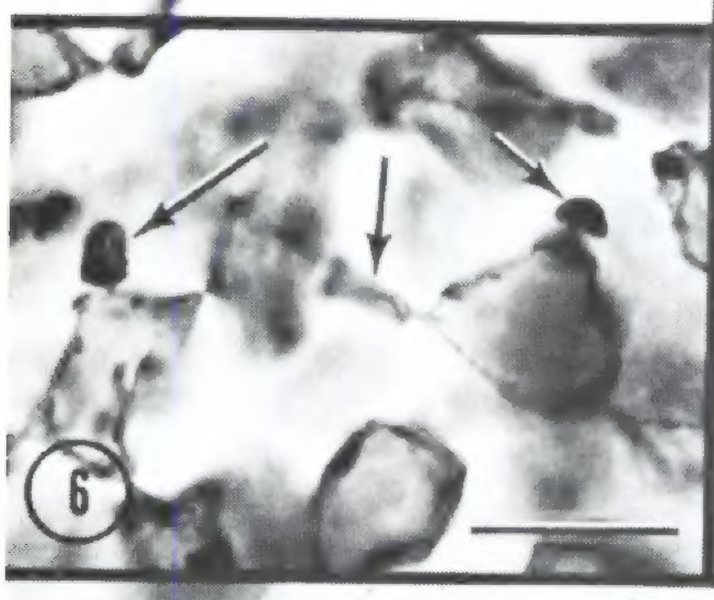

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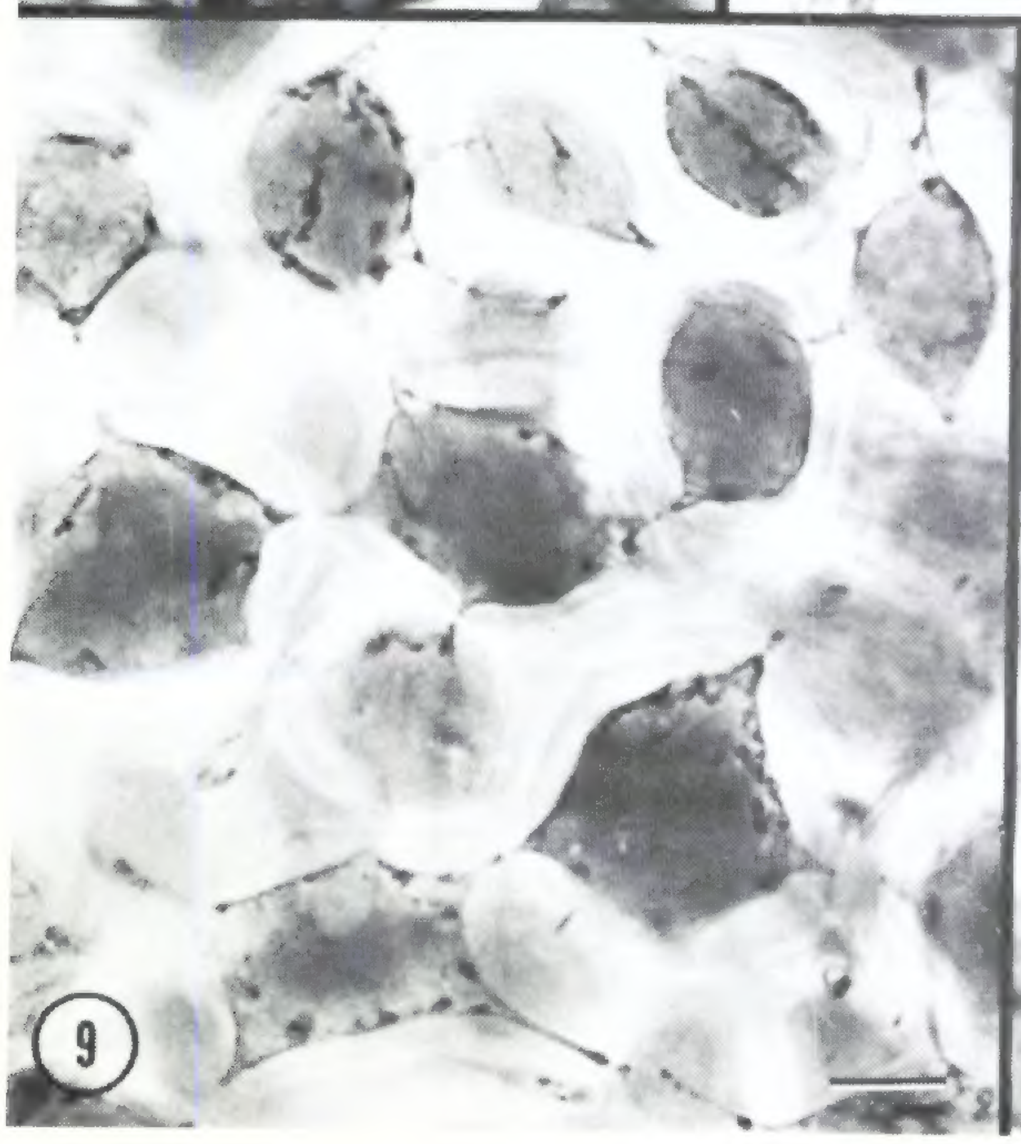

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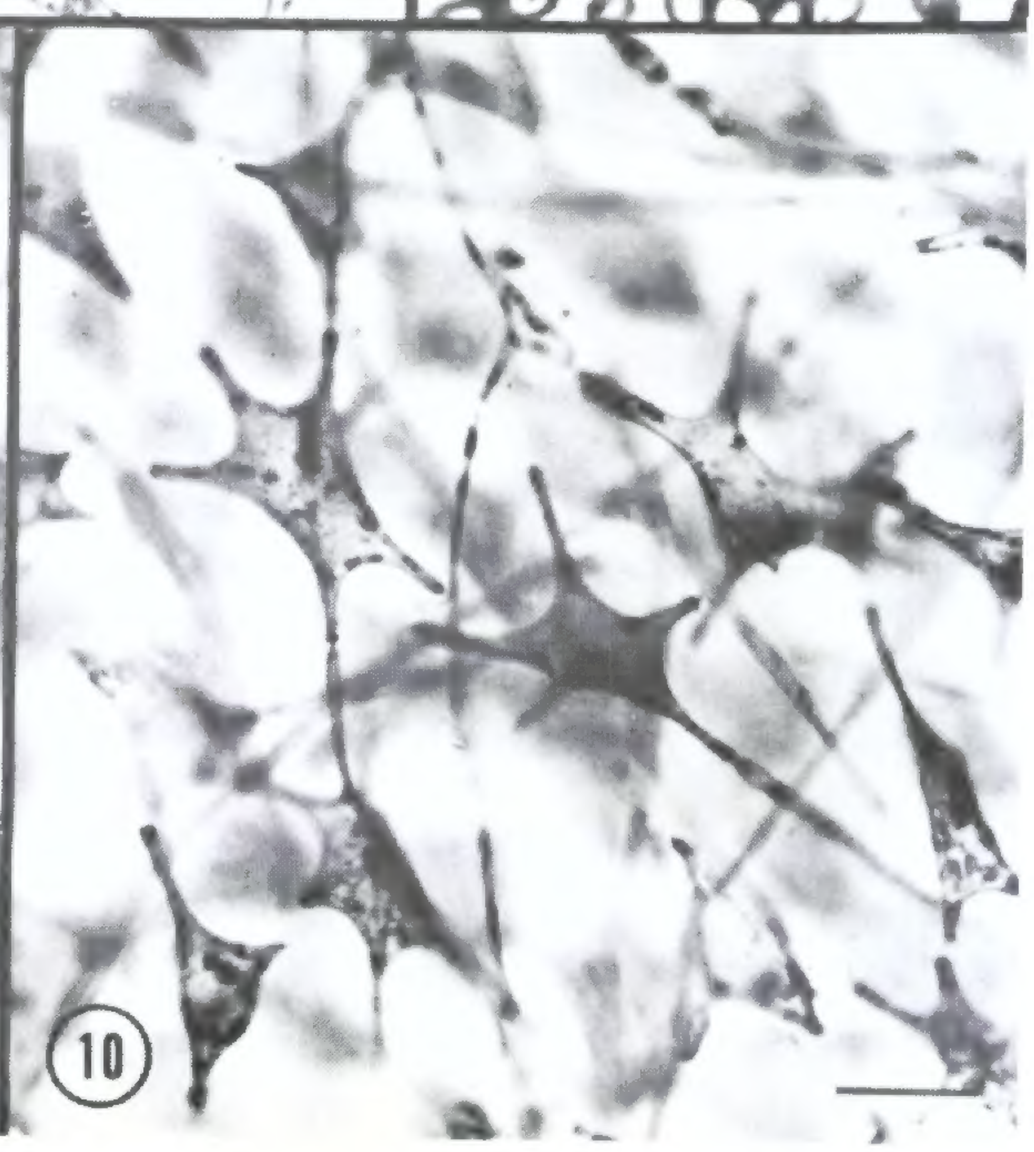

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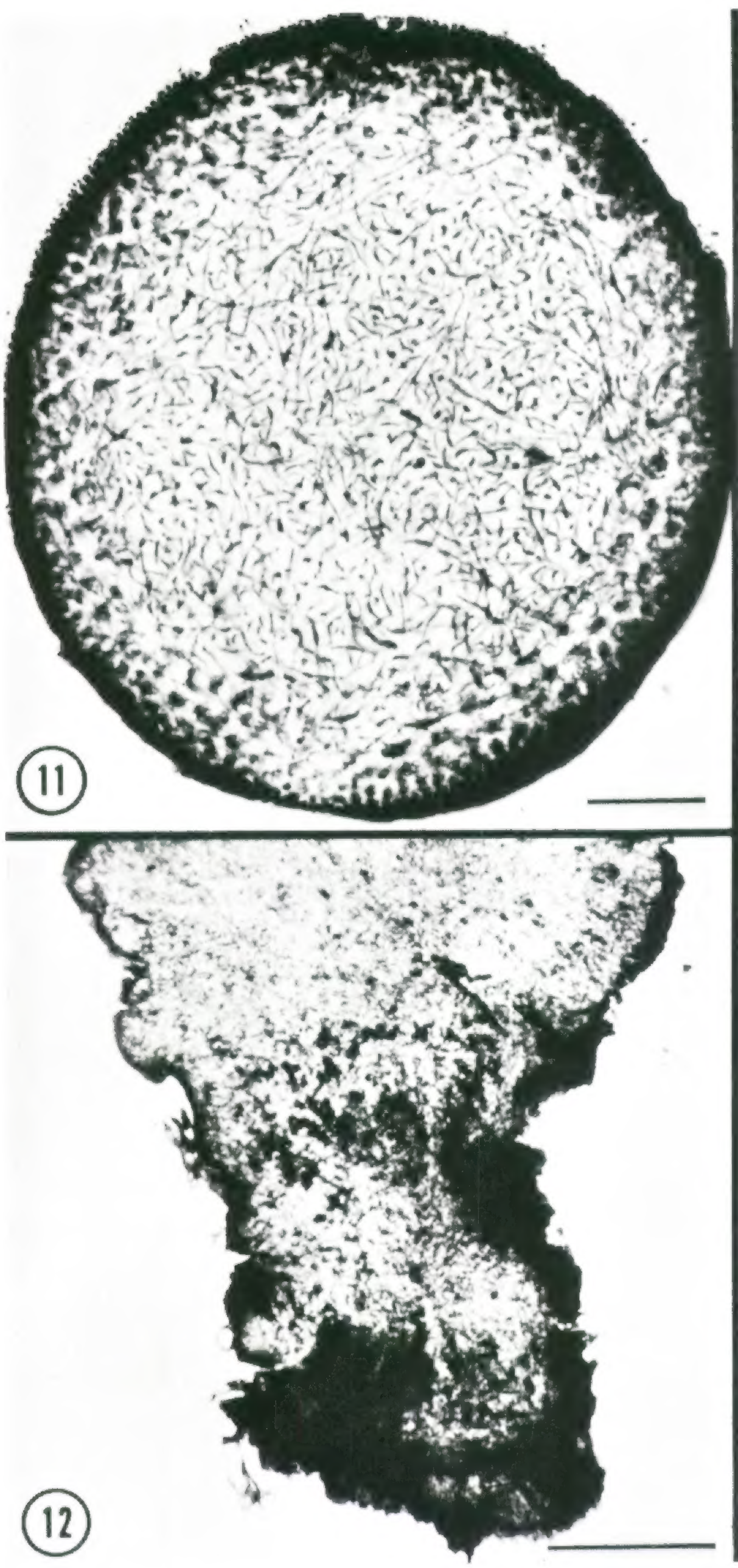


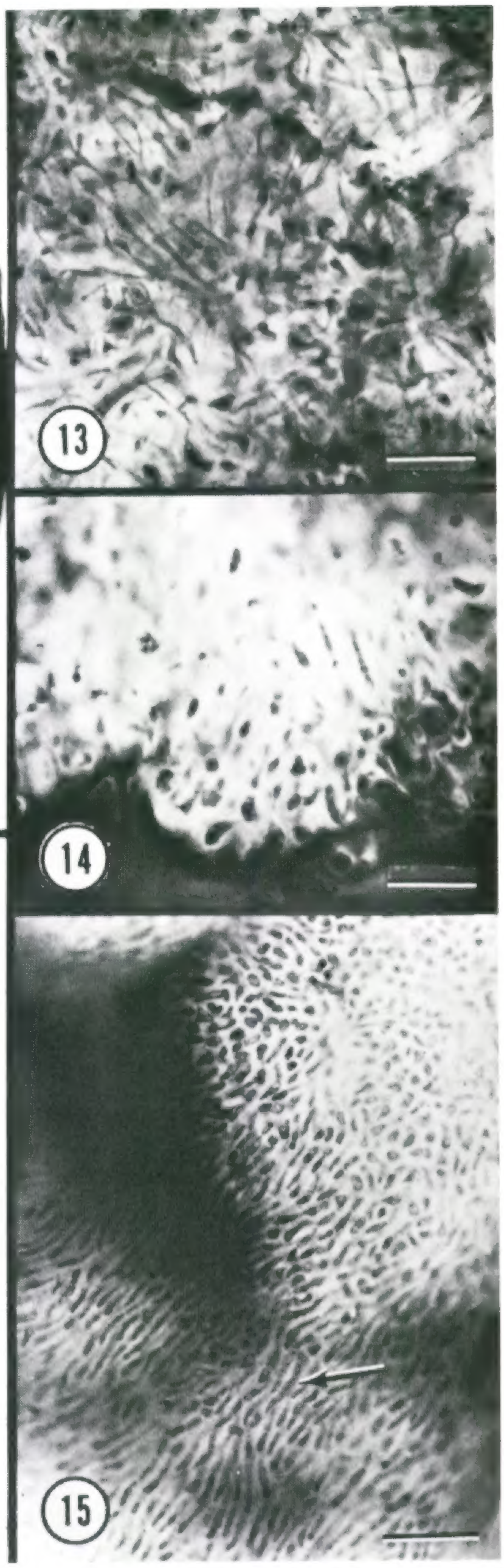


FIG. 11–15. Anatomy of the stipe and holdfast.—11, cross section of the stipe; scale, 100 μm.—12, longitudinal section through the stipe and holdfast; scale, 500 μm.—13, 14, longitudinal sections of holdfast showing the random orientation of the medullary filaments and the outward growth of filaments at the margin; scale, 30 μm.—15, surface view of the base of the holdfast showing outer cortical cells elongated into rhizoidal filaments (arrow); scale, 50 μm.

formed by the meristem may develop into either cortical or medullary cells, depending on the location of their filaments in the blade margin.

The cortex develops from the upper four layers of cells in filaments that are displaced from the meristematic margin. Since the number of cells in the meristem increases by a factor of up to three with each new generation, it would seem that the meristematic surface area should

likewise increase. This does not occur. Only those cells located in the central part of the margin retain their meristematic activity. Cells that are pushed to the sides by the expanding surface cease meristematic activity. These displaced surface cells and the three layers of cells in the filaments behind them differentiate to form the cortex. Cells in the upper two layers round up slightly and form the outer cortex; they do not expand in size and do not form secondary pit connections with neighboring cells. Cells in the third and fourth layers of the displaced filaments form the subcortex, slowly expanding in size and readily forming secondary pit connections with neighboring cells. Subcortical cells have a subglobose to slightly stellate shape when mature (Fig. 9).

The primary medulla develops from cells which are located in filaments remaining behind the meristem. Differentiation of these cells begins when they are located about five layers below the surface. Lateral tension created by the expanding meristematic surface is great enough to cause the branching filaments to become separated except where they are attached by pit connections. Initially, the young cells easily extend to form protrusions in the direction of their pit connections. Secondary pit connections continue to form between the cells by the production of elongated protuberances which extend outward across the necessary distance to connect with neighboring cells. As the expansion continues, the cells appear to be stretched tautly between their pit connections and become stellate in appearance. Young stellate cells are about 10 μm in diameter and, upon maturing, expand to 20–40 μm in size, excluding the stellate arms (Fig. 10). There are usually five or six arms per cell.

Secondary growth occurs mainly in the medullary region of the blade. The space between the stretched primary medullary filaments is filled by numerous, secondarily produced, filiform medullary filaments. These, which may be multicellular, are produced by any of the cells in the subcortex or medulla (Fig. 8). They may extend transversely across the medulla from cortex to cortex or peridermally and parallel to the expanding primary medulla. The filaments frequently terminate their growth by forming secondary pit connections with other vegetative cells. Secondarily derived medullary filaments are responsible for the increase in the thickness of the thallus. They may form anywhere in the plant but are particularly abundant in the basal part of the blade and in the stipe and holdfast.

The structure of the mature stipe is variable. Nearest the blade, the stipe consists of a highly organized cortex and medulla similar to that in the blade (Fig. 11). At the holdfast, the anatomical structure appears to be totally disorganized (Fig. 12). This is caused by the abundant production of secondarily derived medullary filaments which grow downward and intertwine (Fig. 13). At the holdfast, the secondary filaments grow outward around stones and other small objects, aiding attachment (Fig. 14).

Near the edges of the holdfast the normally globose cells of the outer cortex elongate and grow outward like rhizoidal filaments over the substratum (Fig. 15). These rhizoidal cortical cells also appear to assist in anchoring the plant.

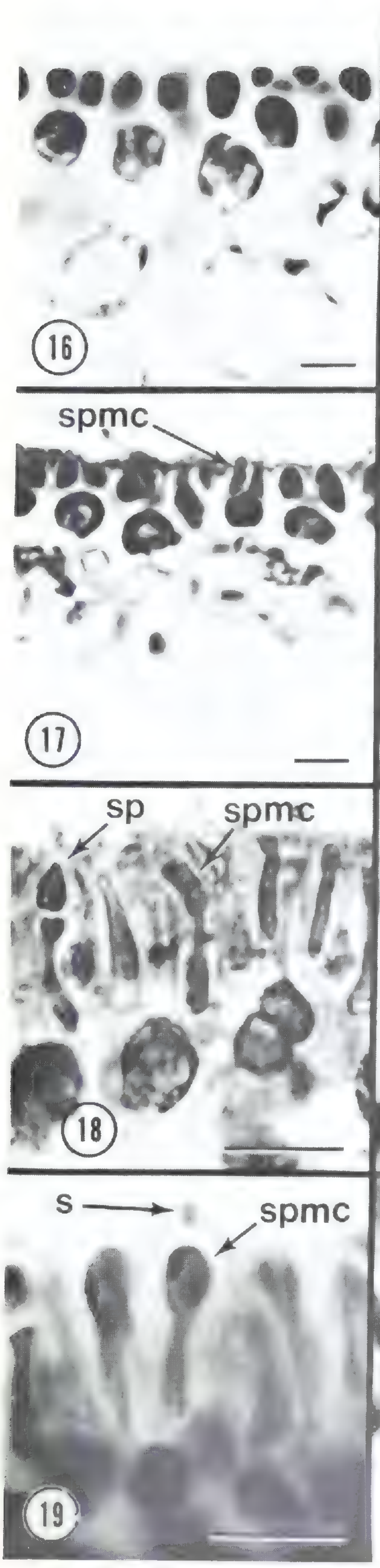
Reproductive Structure. *Cirrulicarpus carolinensis* is dioecious. Male and female plants are found throughout the year, but young sexual fronds occur only in late summer and fall.

In male plants, spermatangia are produced in large soral areas scattered over the surface of the thallus. In young bladelets, spermatangial mother cells and spermatangia begin forming in August, and spermatia are produced from August through November. After this time the spermatangia degenerate, although senescent mother cells remain distinguishable on the fronds throughout the year.

Spermatangia are formed from the cells of the outer cortex. Sterile outer cortical cells are usually subglobose in shape (Fig. 16, 20). On becoming fertile, they elongate slightly and cut off spermatangial mother cells obliquely (Fig. 17, 21). Each outer cortical cell may cleave off up to four spermatangial mother cells (Fig. 22). Each spermatangial mother cell elongates, swells at the tip, and cleaves obliquely to produce one spermatangium which measures 4×5 μm in diameter (Fig. 18). The mother cell may then elongate again and produce a second spermatangium. Spermatia are released through an apical slit directly into the water (Fig. 23). On release, spermatia are 2.0×2.2 μm in size, appear colorless, and are covered only by a mucilage layer (Fig. 19). After spermatium release, only the sheath of the spermatangium is evident.

In the female plants young carpogonial branches develop in late September or early October. Carpogonial branch systems consist of a large supporting cell, one or two three-celled carpogonial branches, and occasionally up to two subsidiary cells (Fig. 28–30). The branch systems develop from initials which are cut off by a subcortical cell inward toward the medulla. Each initial then cuts off one or two other cells (Fig. 24), each of which may divide to form a three-celled carpogonial branch. Often before all of the cells of the carpogonial branches are formed, the cells begin to elongate and become lobed (Fig. 25, 26) and assume the shape characteristic of female reproductive cells of the genus. The initial cell becomes the dumbbell-shaped supporting cell. The first cell of each branch is elongated and lobed, and develops into either a subsidiary cell or the basal cell of a carpogonial branch. The second cell becomes the hypogenous cell of the carpogonial branch; it is usually

FIG. 16–23. Spermatangial development.—16, cross section through the cortex in a sterile area of the blade.—17, cross section through an immature sorus showing the initial stages in the formation of spermatangial mother cells (spmc).—18, cross section through a mature sorus showing the formation of spermatangia (sp).—19, section with a spermatium (s) resting on the thallus surface.—20, surface view of the cortex in a sterile portion of the blade.—21, 22, surface views of spermatangial mother cells formed from outer cortical cells.—23, surface of a fertile area showing the slits (sl) through which spermatia have been released; scale, all 10 μm.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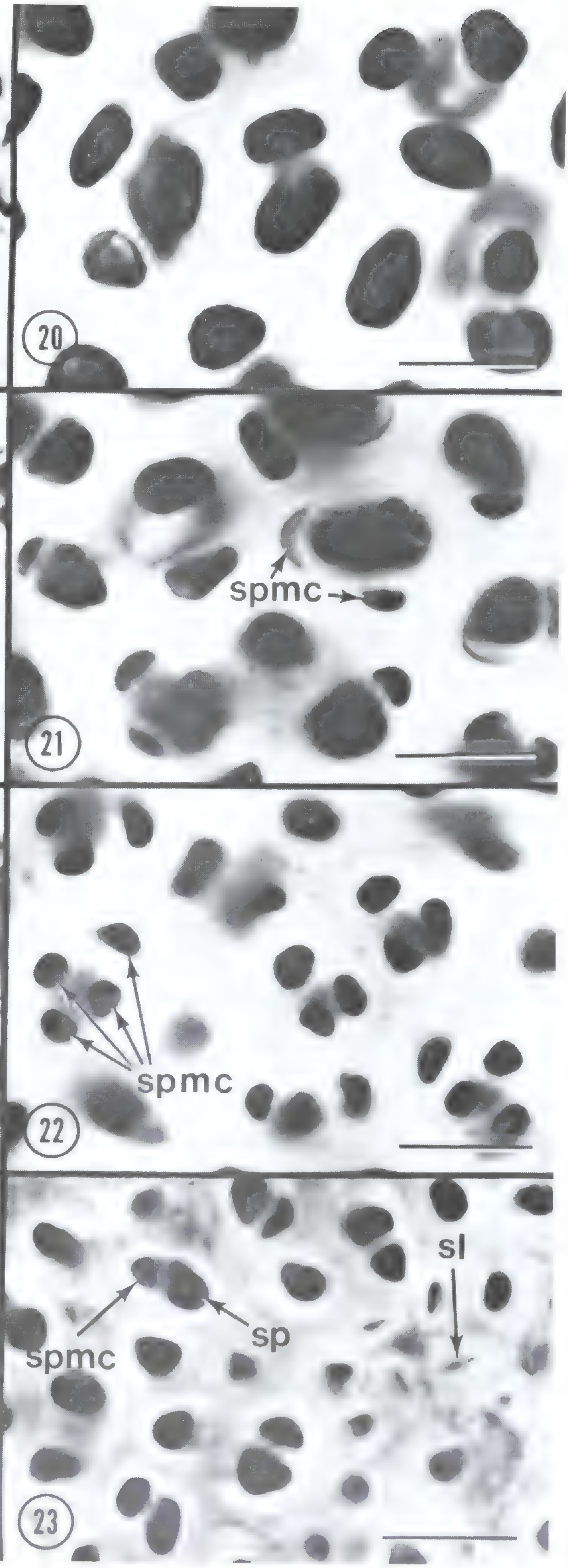
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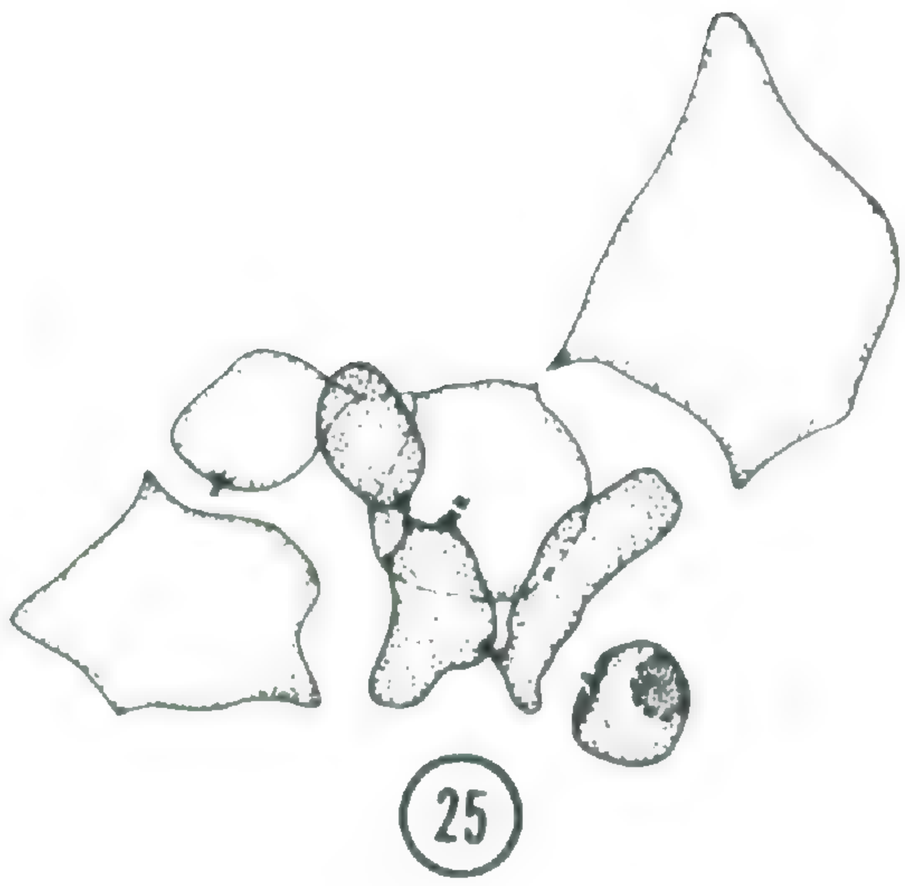
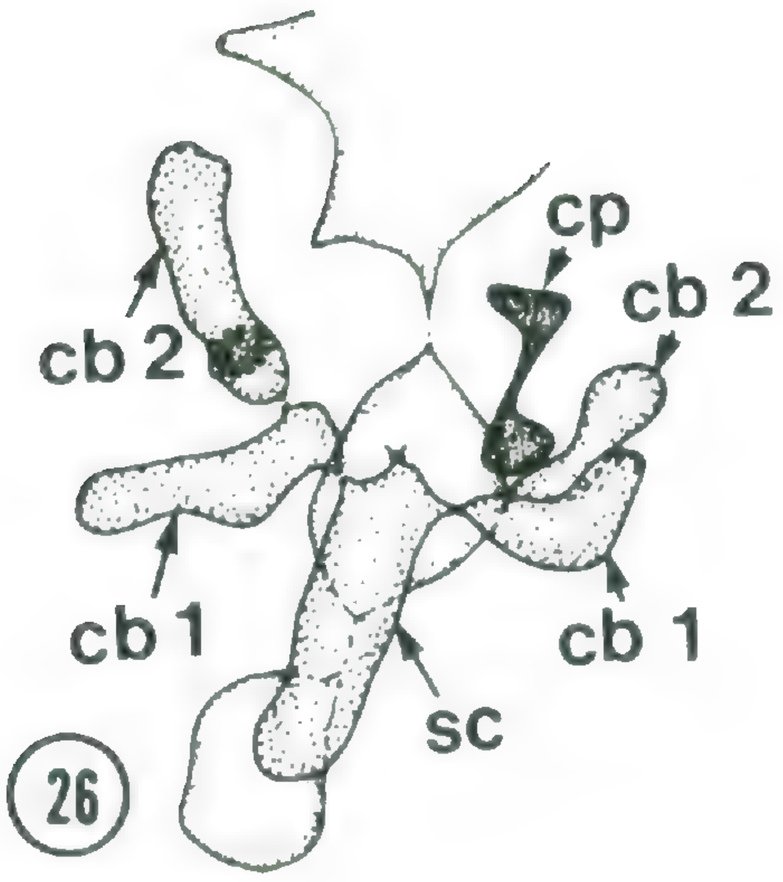
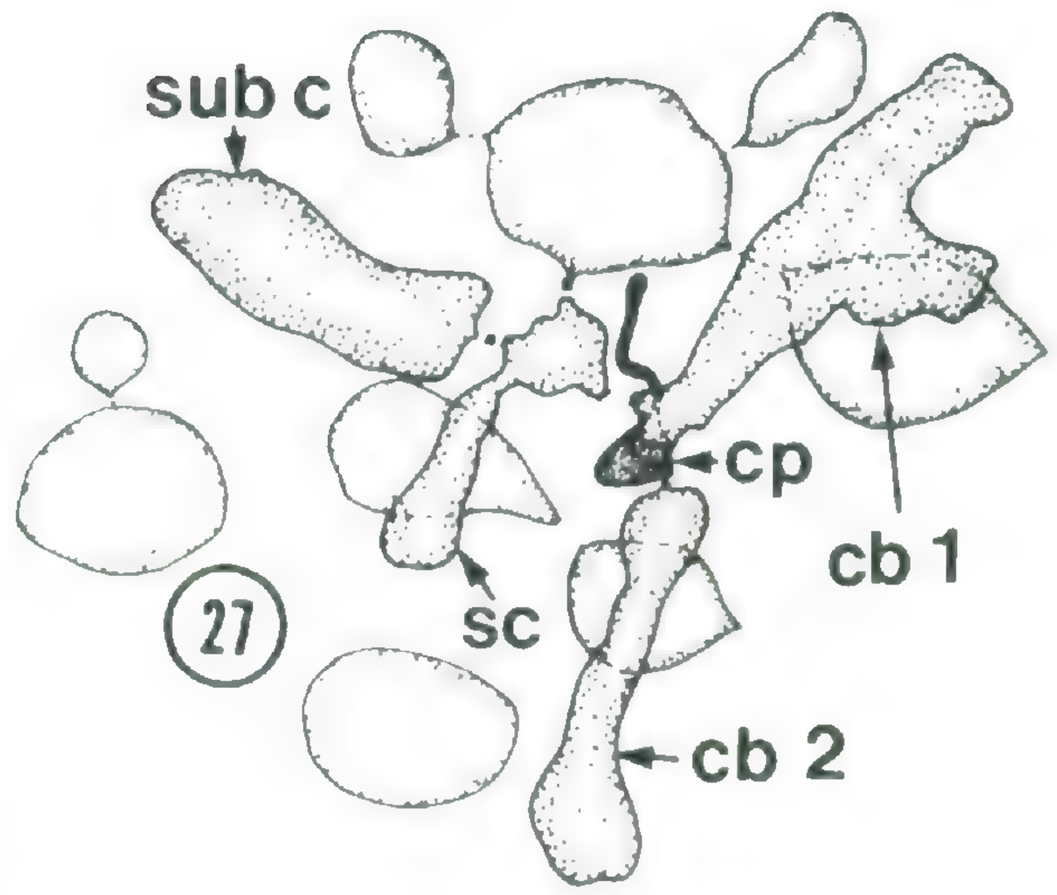






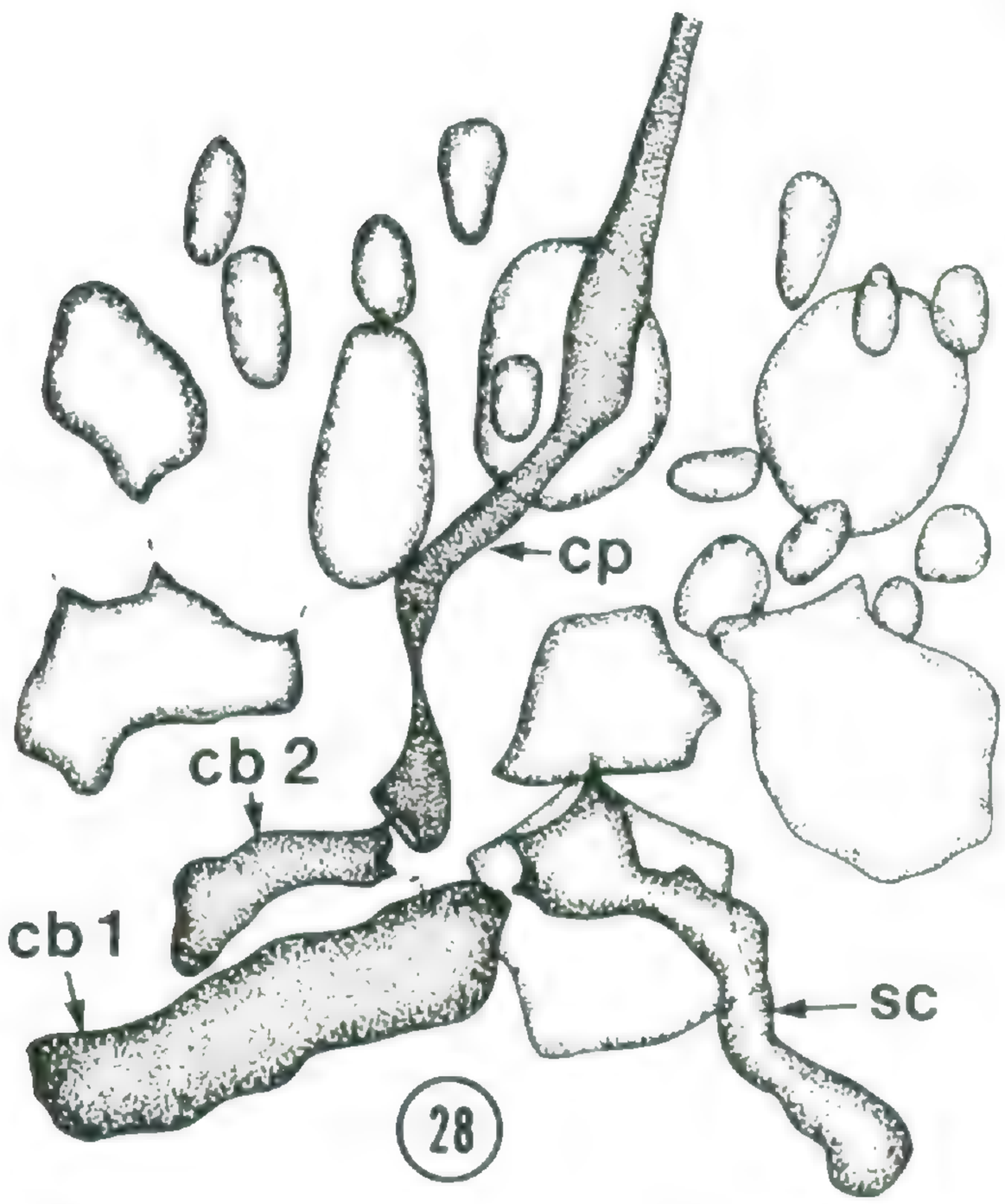


FIG. 24–28. Camera lucida drawings of carpogonial branch system development: sc = supporting cell, cb 1, cb 2, and cp = cells of the carpogonial branch, sub c = subsidiary cells; scale, 30 μm.

slightly smaller but just as elongated and lobed as the basal cell of the carpogonial branch. The third cell forms the carpogonium (Fig. 26–28). A trichogyne is initiated almost immediately but does not elongate until all of the cells of the carpogonial branch are mature (Fig. 26, 27). When two carpogonial branches are present, they form opposite one another on the supporting cell (Fig. 26, 30), and subsidiary cells are rare. This seems to indicate that in *Cirrulicarpus carolinensis* subsidiary cells may correspond to the basal cell of a carpogonial branch which has stopped growth. This has been noted to occur in other members of the Kallymeniaceae by Norris (1957). Mature carpogonial branch systems are covered by papilla-like outgrowths of the outer cortex (Fig. 31).

Actual fertilization or spermatization has not been observed to occur in *Cirrulicarpus carolinensis*, and the process of carposporophyte development appears to be quite unusual. Cells of the carpogonial branch systems do fuse (Fig. 32, 33) but then appear to degenerate. These fusion cells have never been seen producing either primary or secondary gonimoblast filaments. Instead, filaments that resemble secondary gonimoblast fila-

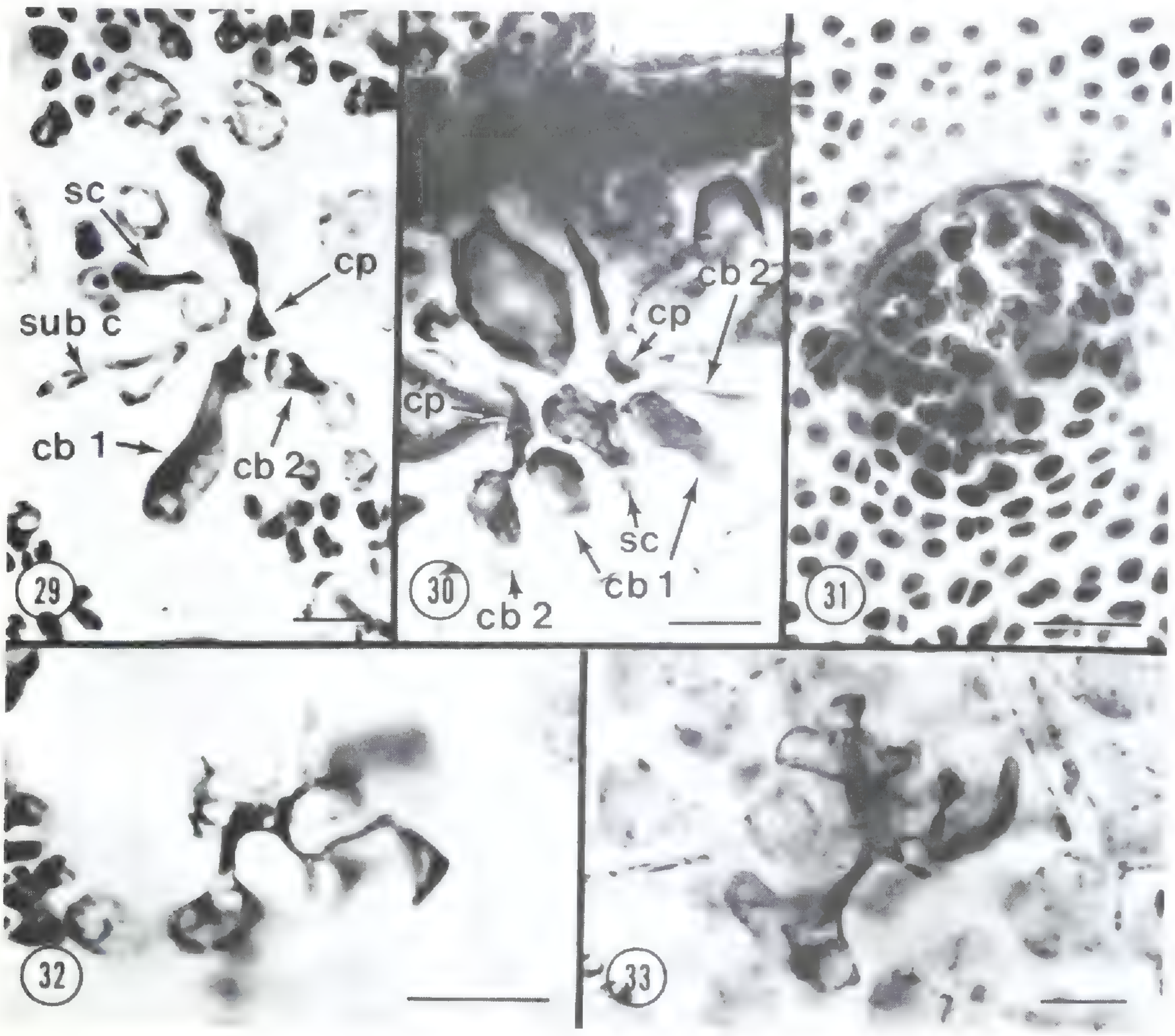


FIG. 29–33. Female reproductive structures.—29, monocarpogonial branch system; scale, 20 μm.—30, dicarpogonial branch systems; scale, 20 μm.—31, surface view of papilla covering a carpogonial branch system; scale, 20 μm.—32, 33, fusion cells formed from the cells of the carpogonial branch system; scale, 30 μm.

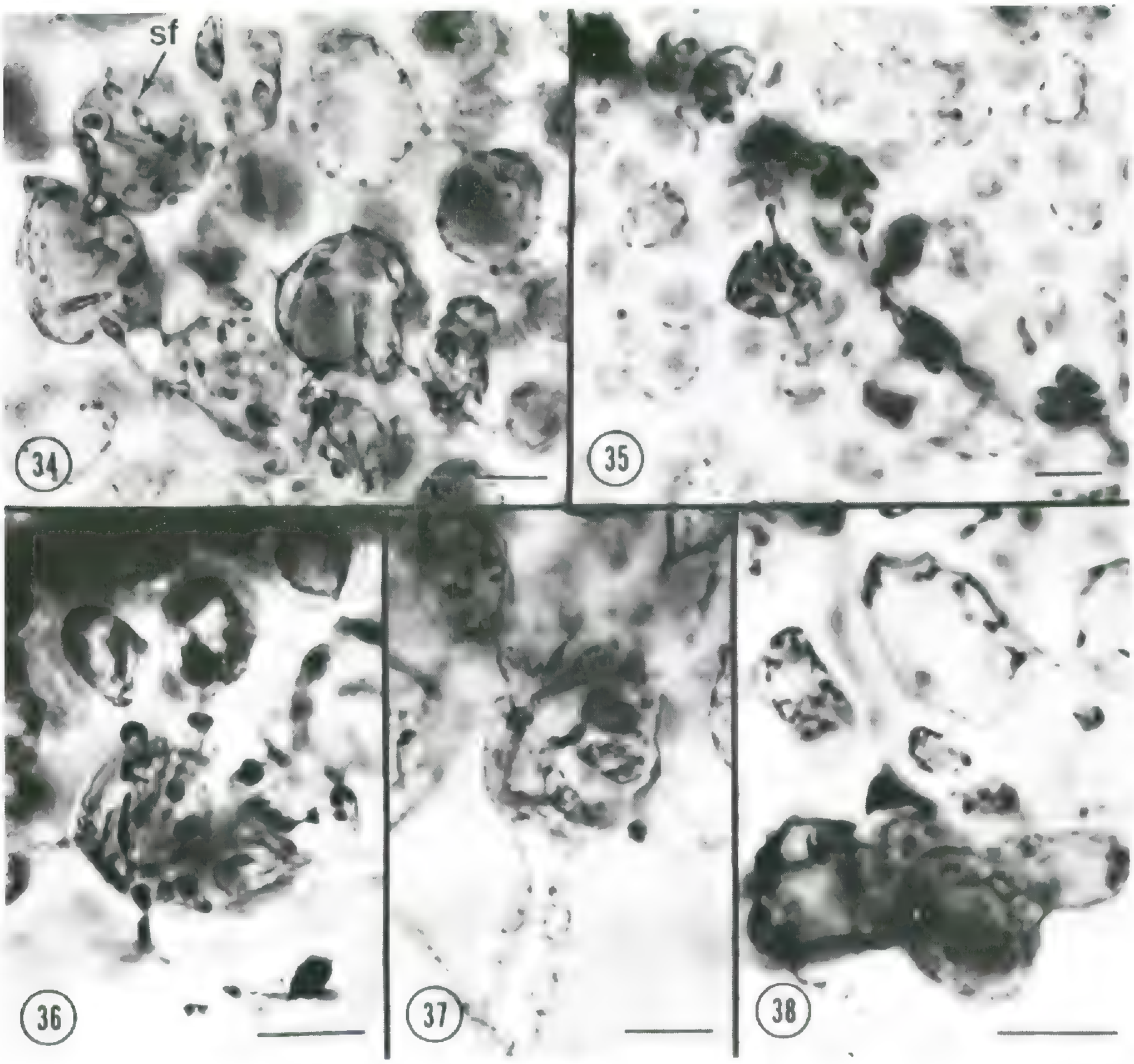


FIG. 34–38. Cell penetration.—34, peel preparation showing the spread of penetrating short-celled filaments (sf) through the subcortex.—35, infested cortical cells below a scratch on the surface of the thallus.—36, 37, single subcortical cells which have been penetrated and infested by short-celled filaments.—38, a carpogonial branch system penetrated and infested by short-celled filaments; scale, all 20 μm.

ments develop from vegetative cells. These filaments, which are lightly staining and short-celled, appear to perform two functions: (1) they penetrate and infest vegetative and reproductive cells in the thallus, leading to the disintegration of these cells; or (2) they form an extensive network of cells which eventually form carposporangia. Filaments penetrating other cells may not necessarily be able to form carposporangia, but filaments forming carposporangia can always penetrate and infest nearby cells.

When the surface of the alga is scratched or in some way damaged, the cortical and subcortical cells beneath are immediately penetrated by short-celled filaments which arise from neighboring cells (Fig. 34). Frequently only the cells directly under the line of pressure are invaded (Fig. 35). At times, particular subcortical cells will be invaded by filaments produced by neighboring cells for no obvious reason (Fig. 36, 37).

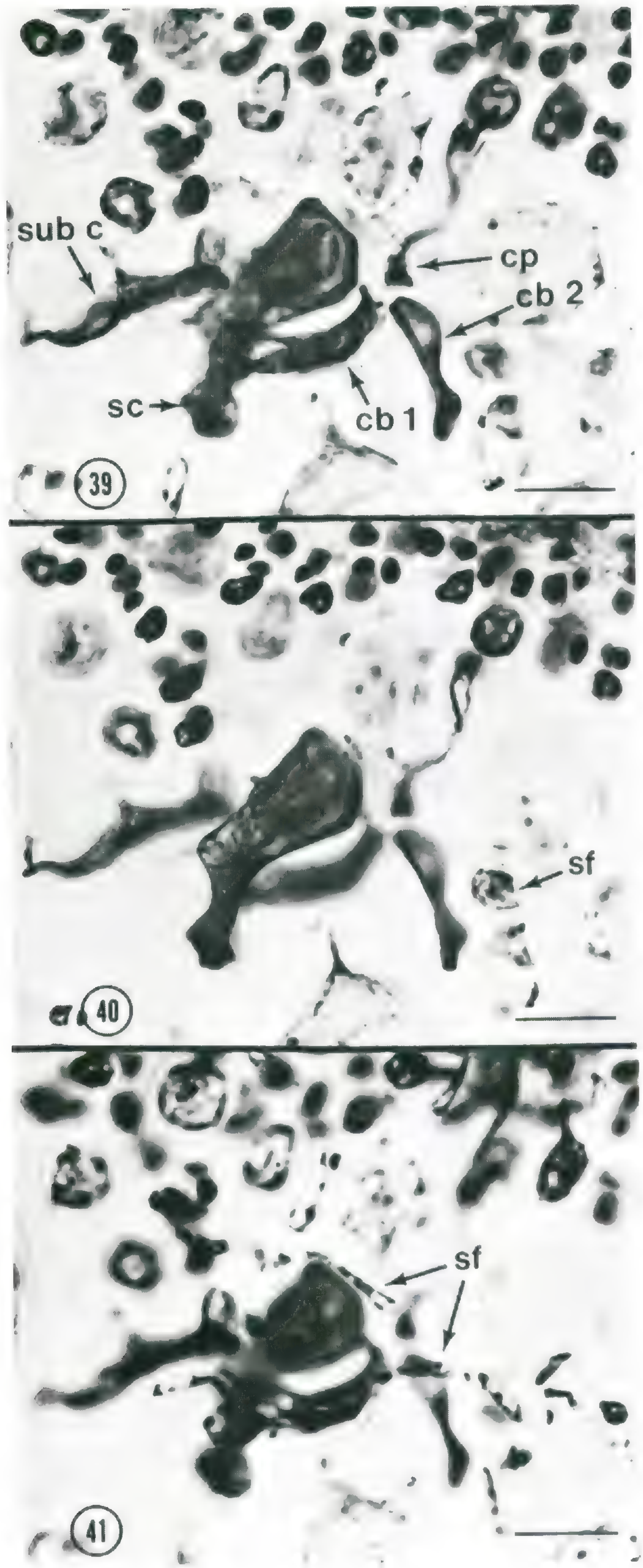
The same filaments also penetrate and appear to digest nutrient-rich reproductive cells (Fig. 38).

Short-celled filaments that form carposporangia usually develop from cells of the subcortex. Frequently they arise from subcortical cells that are located next to a carpogonial branch system and then proliferate in the area around it (Fig. 39–41). However, just as often, filaments develop from vegetative cells which are removed by numerous pit connections from the carpogonial branch systems (Fig. 42). Once initiated, the filaments wind their way between the vegetative cells of the cortex for a considerable distance (Fig. 43). The presence of these filaments seems to stimulate the initiation of new filaments by the surrounding vegetative cells. Eventually the density of the short-celled filaments reaches a saturation level in both the cortex and medulla. When this point is reached, short, almost spherical cells are produced both terminally and laterally by the filaments (Fig. 44). These cells then initiate chains of cells that rapidly increase in pigment content and in size and mature into carposporangia (Fig. 45). The swelling of the carposporangia causes the cystocarp to protrude on both sides of the thallus and the carposporangial chains to appear as clusters separated by gonimoblast filaments and stretched vegetative cells (Fig. 46).

Young cystocarps first appear as a gray discoloration in the thallus surface. At this stage the cortex and medulla are infested by the lightly pigmented, short-celled filaments (Fig. 47). Such regions contrast sharply with the clear cortical and medullary tissues of sterile areas of the thallus (Fig. 48). When deeply-pigmented carposporangia develop, the cystocarp becomes deep red in color.

Young cystocarps develop in the mid-to-outer portions of the fronds. They are large (up to 3 mm in diameter) and oval in shape (Fig. 49). Normally cystocarps are solitary or grouped irregularly on the fronds (Fig. 50, 51) and occasionally a ring of cystocarps is formed (Fig. 52). A central cystocarp is usually present, and one or two rings of smaller, individual or confluent cystocarps surround it. The rings appear to be initiated by some influence of the central cystocarp and are preceded in development by a gray region formed in a halo around the central cystocarp (Fig. 50). These gray areas are identical to immature cystocarps and are caused by the outward growth of short-celled filaments from the central cystocarp. When the surrounding area is saturated with filaments, carposporangia are initiated and the area deepens in color as the ring of cystocarps forms. A second ring of cystocarps may then develop in an identical manner.

Carpospores are released from mature cystocarps through cracks in the surface layers. Before release, portions of the outer cortex around the developing cystocarp degenerate, and as the carposporangia enlarge, the weakened areas in the cortex split open (Fig. 53). Each cystocarp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may release spores over a period of several weeks, after which the cystocarps continue to grow outward and become wart-like in appearance (Fig. 54). Senescent cystocarps are often present on the lower parts of female plants long after the first period of sexual maturity.

Life History. Because tetrasporophytes of *Cirrulicarpus carolinensis* were not found in the field, carpospores of this alga were cultured in the laboratory to determine if a tetrasporophyte phase existed in the life history. The details of these studies will be reported in a later paper, and only a brief summary is included here.

Carpospores, obtained from plants of *Cirrulicarpus carolinensis* collected between October and December, were released from cystocarps in uniform round sprays (Fig. 55). The spores measured 9 × 11 μm in diameter. Germination was of the "typus filamentosus mediatus" (Inoh, 1947) and of the "persistent-spore type" (West, 1968) and proceeded in both unipolar and bipolar fashion (Fig. 56). A heterotrichous system consisting of closely branched prostrate filaments and sparsely branched upright filaments soon developed (Fig. 57).

As the germlings grew older, the prostrate system became very extensive. It consisted of axial filaments with closely branched lateral filaments (Fig. 58) and was similar in appearance to *Hymenoclonium serpens* (Crouan & Crouan) Batters. Lateral branches continued to divide until a network of very closely appressed cells was produced. The elongated shape of the axial cells contrasted with the short cells of the lateral filaments (Fig. 59). Close examination of these prostrate networks revealed that the cells of neighboring filaments frequently fuse with one another (Fig. 60). Similar fusions have been reported to occur in many members of the Corallinaceae (Rosenvinge, 1917; Cabioch, 1970, 1971), in *Cruoriopsis* and in *Rhododermis (Rhodophysema) elegans* (Rosenvinge, 1917), and in *Kallymenia* (Codomier, 1972, 1973).

The prostrate system was initially monostromatic, but as maturation proceeded, filaments of the lower layer occasionally branched upward and formed a second layer on top of the first (Fig. 61). This process continued until a thick layered crust about four cells deep developed. These thickenings were usually restricted to small areas on the original monostromatic network. Occasionally cells in the upper layers of the thickenings initiated short, erect filaments which were terminated by cap-like or hair-like cells (Fig. 62). Most often these erect filaments remained as crusts, but occasionally, after long periods in culture, certain filaments grew upward and formed erect, multiaxial, gametophytic blades, identical to small, field-collected plants of *Cirrulicarpus carolinensis* (Fig. 63). Thus, the life history appears to have no tetrasporophyte generation, and germlings from carpospores may be considered protonemal in nature.

FIG. 39–41. A carpogonial branch system viewed at three focal planes. A short-celled filament has originated from the neighboring subcortical cell and is actively proliferating in the vicinity of the carpogonial branch; scale, 20 μm.

DISCUSSION AND CONCLUSIONS

Because of its vegetative structure, the number and arrangement of cells in the carpogonial branch system, and cystocarp anatomy, *Cirrulicarpus carolinensis* clearly belongs in the family Kallymeniaceae. The new species is placed in the genus *Cirrulicarpus* because it is complanate and cartilaginous and has a repeatedly branched thallus which is narrowly cuneate below and rounded at the apices. The plant has a filamentous medullary system, a carpogonial branch system that consists of elongated or lobed cells, and cystocarps that occasionally form in rings.

The vegetative anatomy of *Cirrulicarpus carolinensis* corresponds with the second of three kinds of thallus structure in the Kallymeniaceae

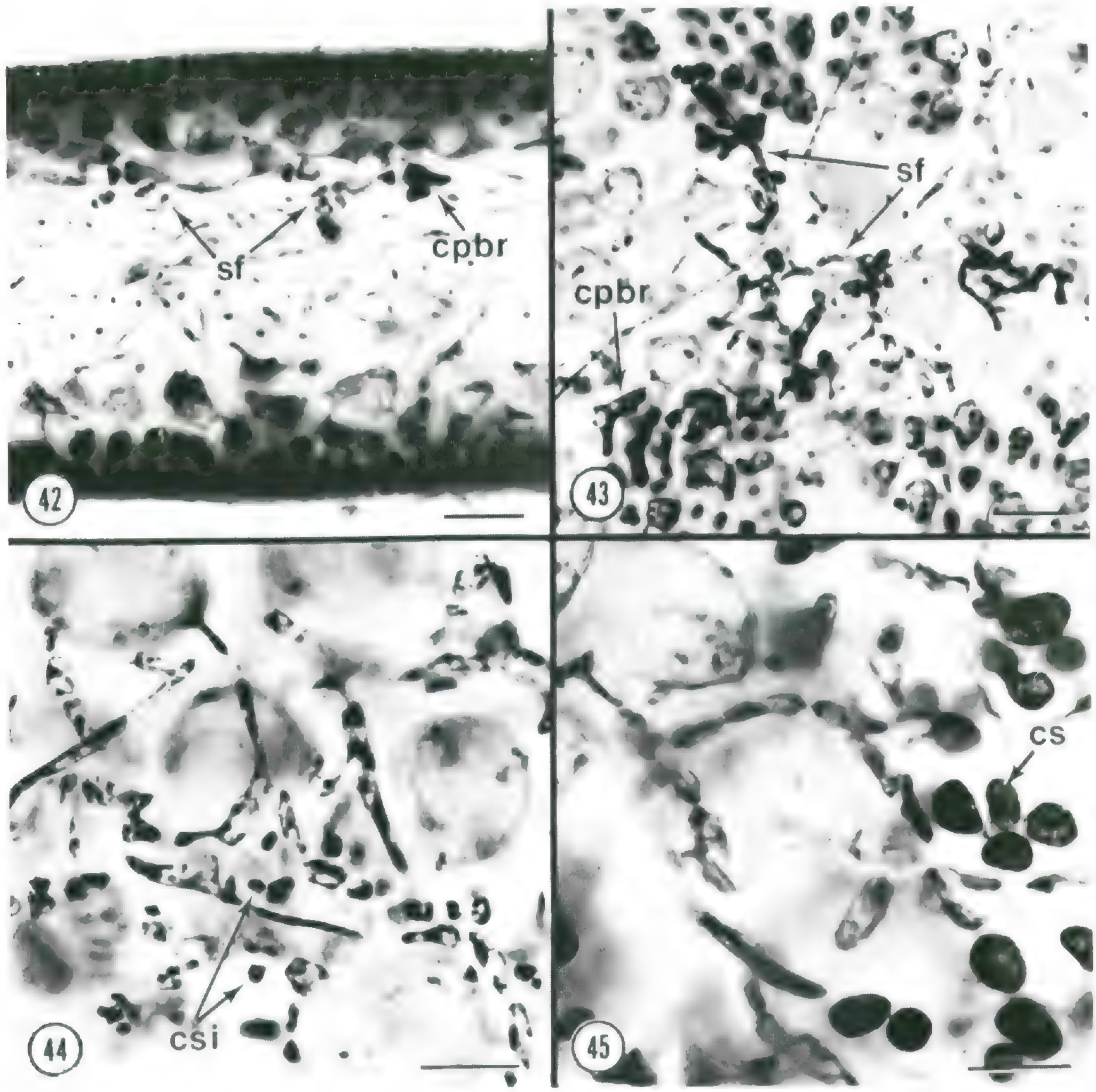
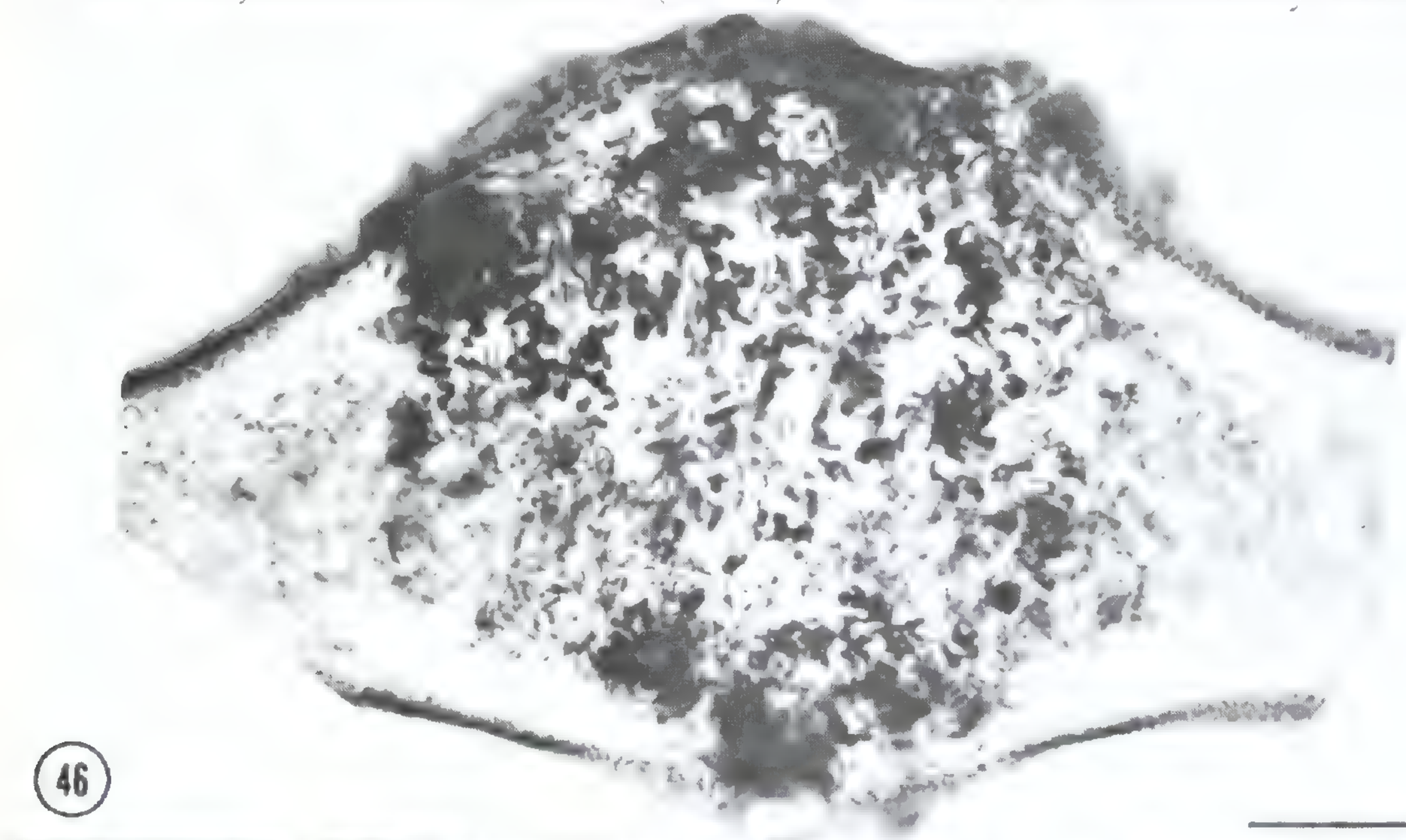
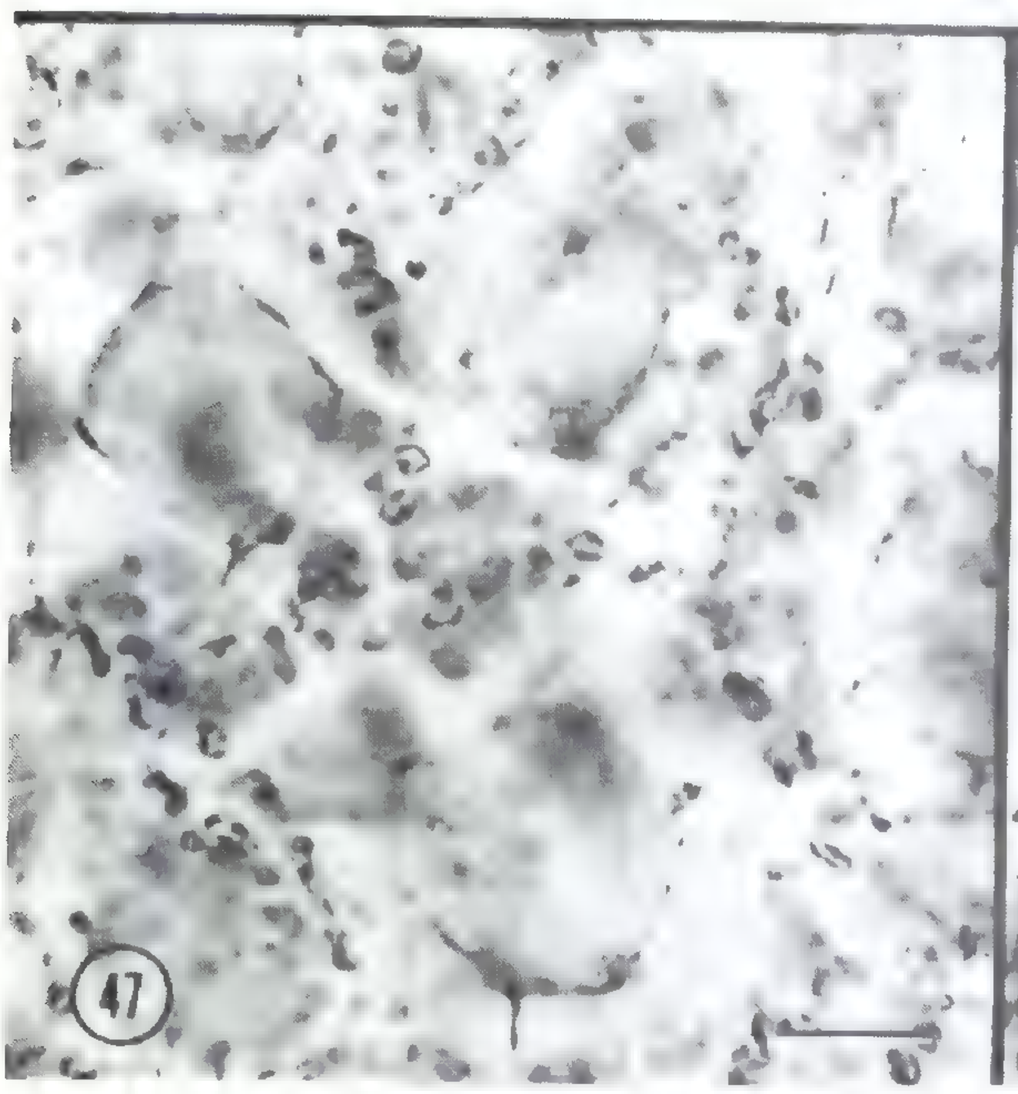


FIG. 42–45. Gonimoblast development.—42, the initiation of short-celled filaments from subcortical cells near and far from the carpogonial branch system (cpbr); scale, 20 μm.—43, a peel preparation showing short-celled filaments originating near a carpogonial branch system and winding their way between the preexisting vegetative cells; scale, 30 μm.—44, short-celled filaments originating from subcortical cells and growing thickly between the vegetative cells. The small, rounded, deeply staining cells (csi) initiate carposporangial chains; scale, 20 μm.—45, short-celled filaments forming a carposporangia (cs) in chains both terminally and laterally; scale, 20 μm.

recognized by Womersley and Norris (1971) wherein the primary medullary cells, while remaining recognizable, become separated by a "profuse and usually loose development of filaments," and the medulla appears essentially filamentous. In *C. carolinensis* stellate cells form the primary medulla and filiform cells the secondary medulla. Primary growth is initiated at the surface of the margin of the flattened frond, and rows of three to four undifferentiated cells lie behind each apical cell before differentiating into stellate cells. Norris (1957, 1964) described the axial filaments as extending to the surface of the growing margin in *Callophyllis*, *Thamnophyllis*, *Kallymenia*, and *Pugetia*, seeming to imply the existence of a surface meristem. In *Glaphrymenia*, another member of the Kallymeniaceae, Norris (1961) described an intercalary meristem





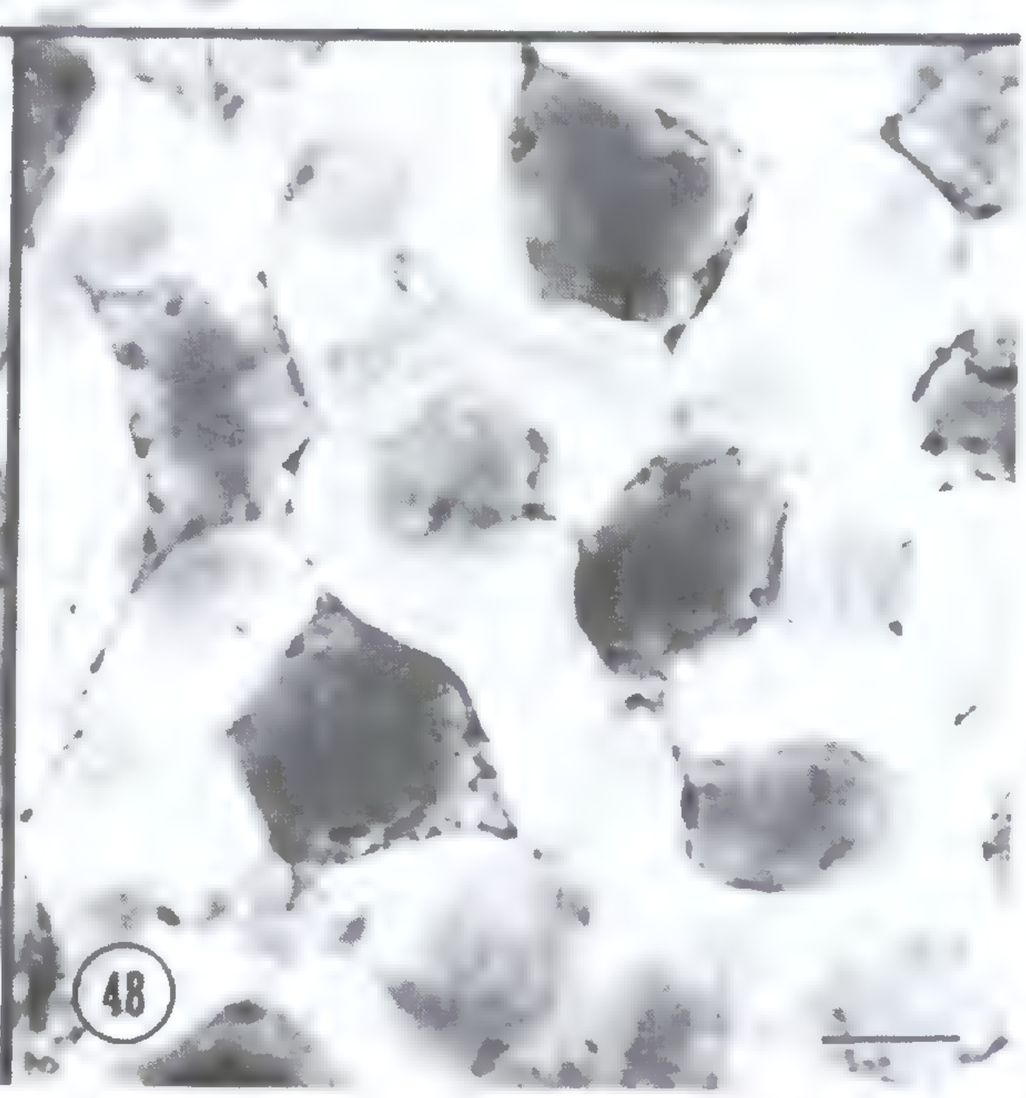


FIG. 46–48. Cystocarp structure and fertile and sterile subcortical regions.—46, a mature cystocarp with carposporangia in clusters separated by stretched vegetative cells and short-celled gonimoblast filaments; scale, 0.2 mm.—47, 48, peel preparations of the subcortex in fertile and sterile areas of the thallus; scale, 20 μm.

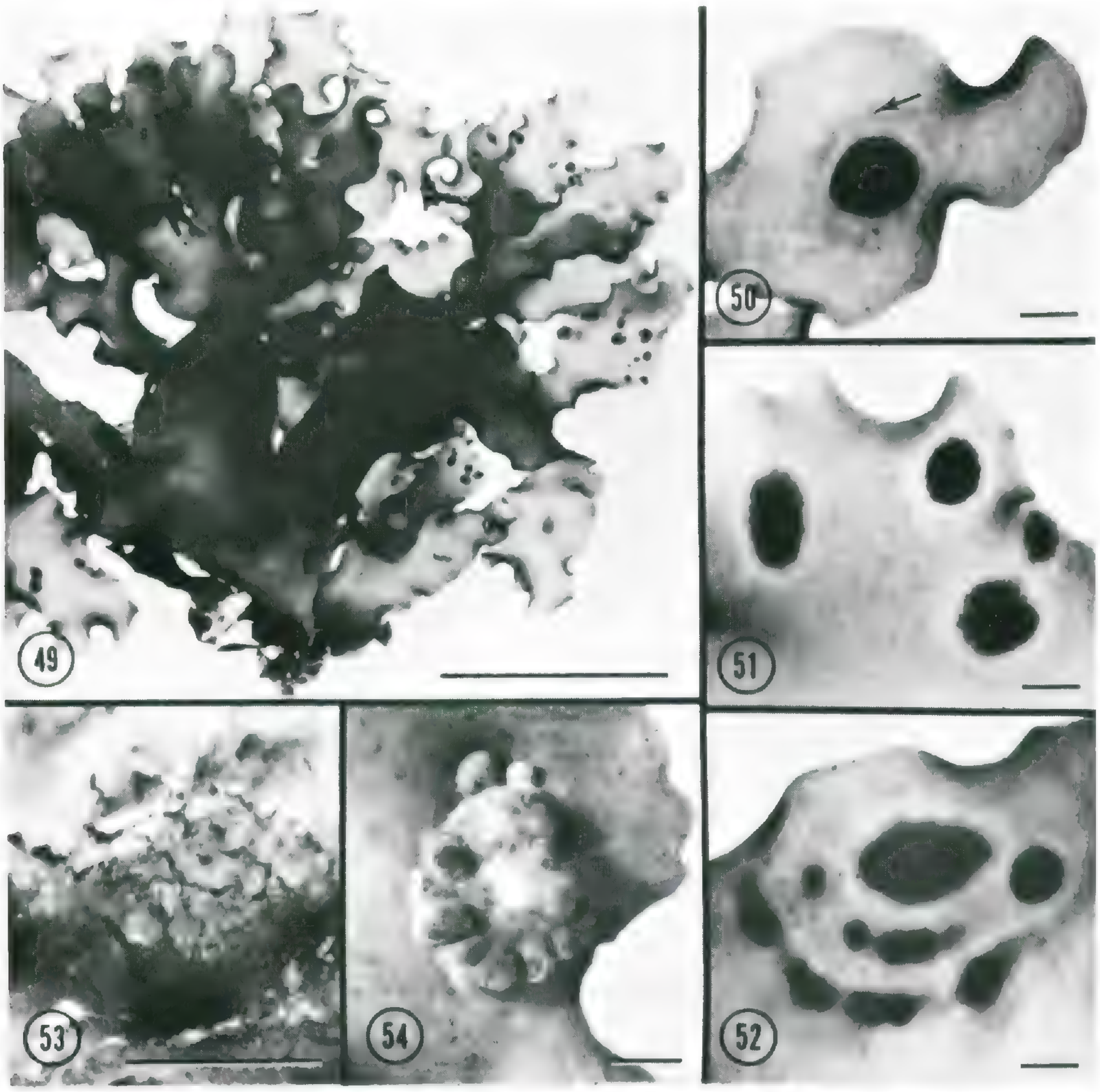


FIG. 49–54. Cystocarp morphology.—49, a female plant with young cystocarps scattered in the upper portion of the blade; scale, 3 cm.—50, a solitary young cystocarp with a gray halo (arrow) around it; scale, 1 mm.—51, young cystocarps in a scattered arrangement; scale, 1 mm.—52, a mature cystocarp with two concentric cystocarpic rings situated around the lower side; scale, 1 mm. —53, the surface of a mature cystocarp showing the cracks through which carpospores will be released; scale, 1 mm.—54, an aging cystocarp that has already released carpospores (white area) and is becoming wart-like; scale, 1 mm.

located in the terminal row of cells at the growing margin. Secondary growth in *Cirrulicarpus carolinensis* occurs through the production of filiform medullary filaments from subcortical and stellate cells throughout the thallus, and these filaments are responsible for its thickening. In the holdfast the secondary filaments are extremely dense and grow downward aiding in attachment of the blade as was also described for *Glaphrymenia pustulosa* by Norris (1961). Moreover, in *C. carolinensis* cells of the outer cortex grow downward in a rhizoidal fashion also aiding in the attachment of the blade to the substrate.

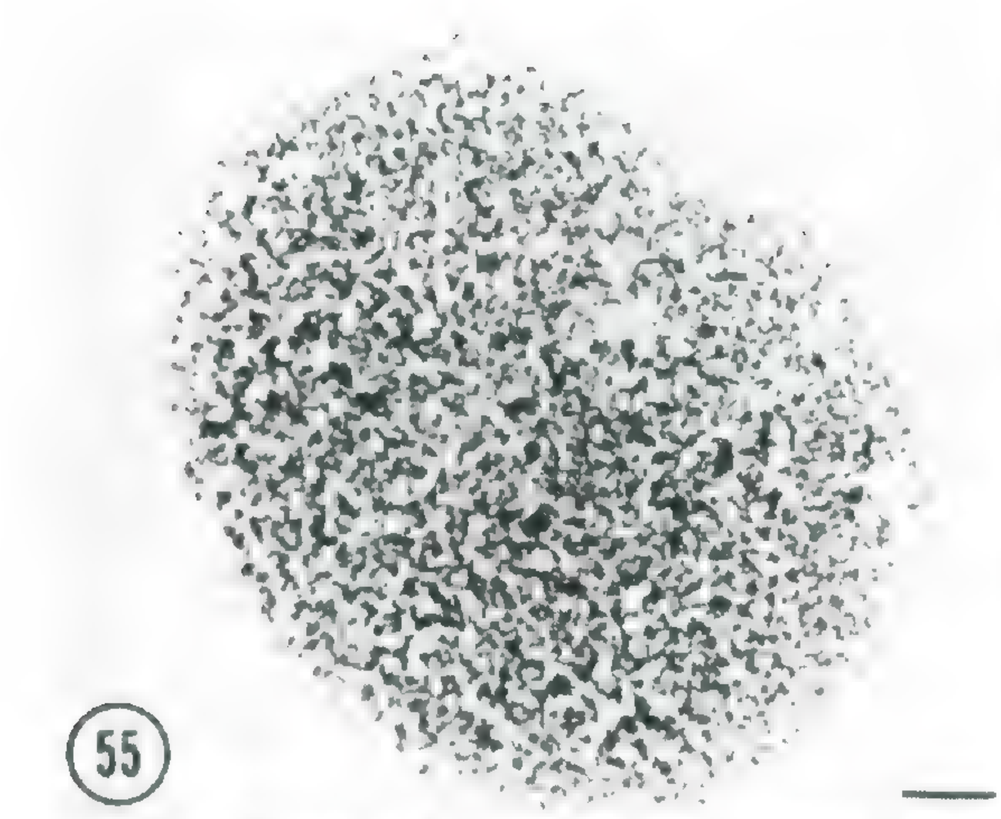
The production of sexual structures in *Cirrulicarpus carolinensis* occurs in the fall on the North Carolina coast. Development of both spermatangia and carpogonia appears to be normal. Carpogonial branch systems

develop in a pattern similar to those described for other members of the Kallymeniaceae (Norris, 1957). Spermatangia, which have seldom been studied in this family, follow a pattern of development somewhat similar to that described for *Cystoclonium purpurascens* in the Gigartinales by Kylin (1923). The release of spermatia in *Cirrulicarpus carolinensis* occurs from August to December and brackets the time of carpogonial branch maturation in October. This timing would seem to insure fertilization, particularly since numerous individuals of both sexes are found in the field. However, no conclusive evidence of fertilization was found. Fusion cells, similar to those described by Norris (1957) as post-fertilization stages for many members of the Kallymeniaceae, are present but appear to be degenerate. Carposporophyte development appears to be initiated by vegetative cells. The production of gonimoblast filaments from vegetative cells might indicate that fertilization has taken place, but filaments are frequently initiated by cells that are quite distant from a carpogonial branch system. The only visible connection between the two is through preexisting vegetative cells and their pit connections—an unlikely path for the transfer of a diploid nucleus.

In *Cirrulicarpus carolinensis* short-celled gonimoblast filaments may either form carposporangia or penetrate and infest vegetative or reproductive cells apparently to digest their contents. Since similar penetrating filaments are produced by vegetative cells in wounded areas of the thallus, one might speculate that both carposporophyte development and wounding produce a similar kind of stress on the alga.

The production of gonimoblast filaments from vegetative cells has rarely been reported in the Florideophycidae and, then, only in the Cryptonemiales and Gigartinales. In *Kallymenia reniformis*, Hommersand and Ott (1970) found that gonimoblast filaments arose from vegetative cells that had been contacted by connecting filaments. Kraft (1973) reported similar findings in *Cubiculosporium koronicarpus*. In *Mycodea carnosa* and several species of *Neurophyllis*, Kraft (1974) reported the production of carposporangia from vegetative cells that (1) appeared to be in direct contact with gonimoblast filaments, (2) were "adjacent to cells contacted by gonimoblast filaments," or (3) were "removed by a distance of many pit connections" from cells initially in contact with gonimoblast filaments. In all of the species mentioned a true auxiliary cell was also reported. *Cirrulicarpus carolinensis* has the distinctive characteristic of having both gonimoblast filaments borne on vegetative cells and also of having no true auxiliary cells.

Mature cystocarps of *Cirrulicarpus carolinensis* are composed of clusters of carposporangia in chains separated by vegetative and gonimoblast filaments very much like the cystocarps of many other members of the Kallymeniaceae. However, cystocarps of *C. carolinensis* may also occur in small clusters or in rings, as is characteristic of other members



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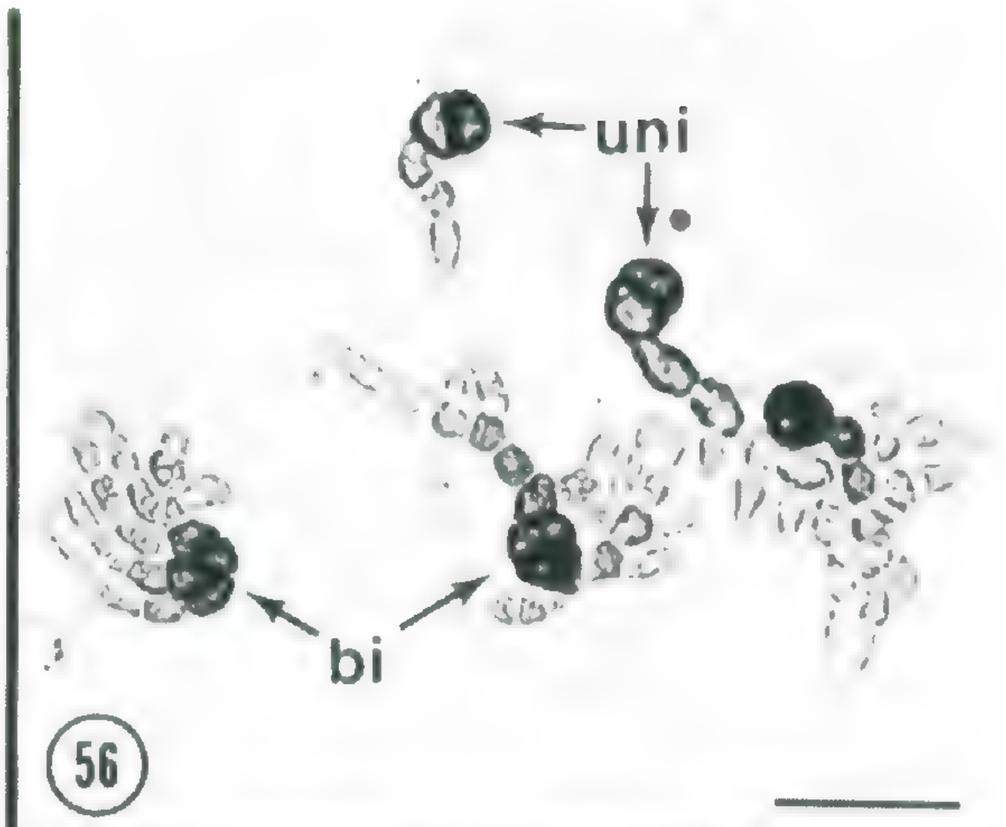

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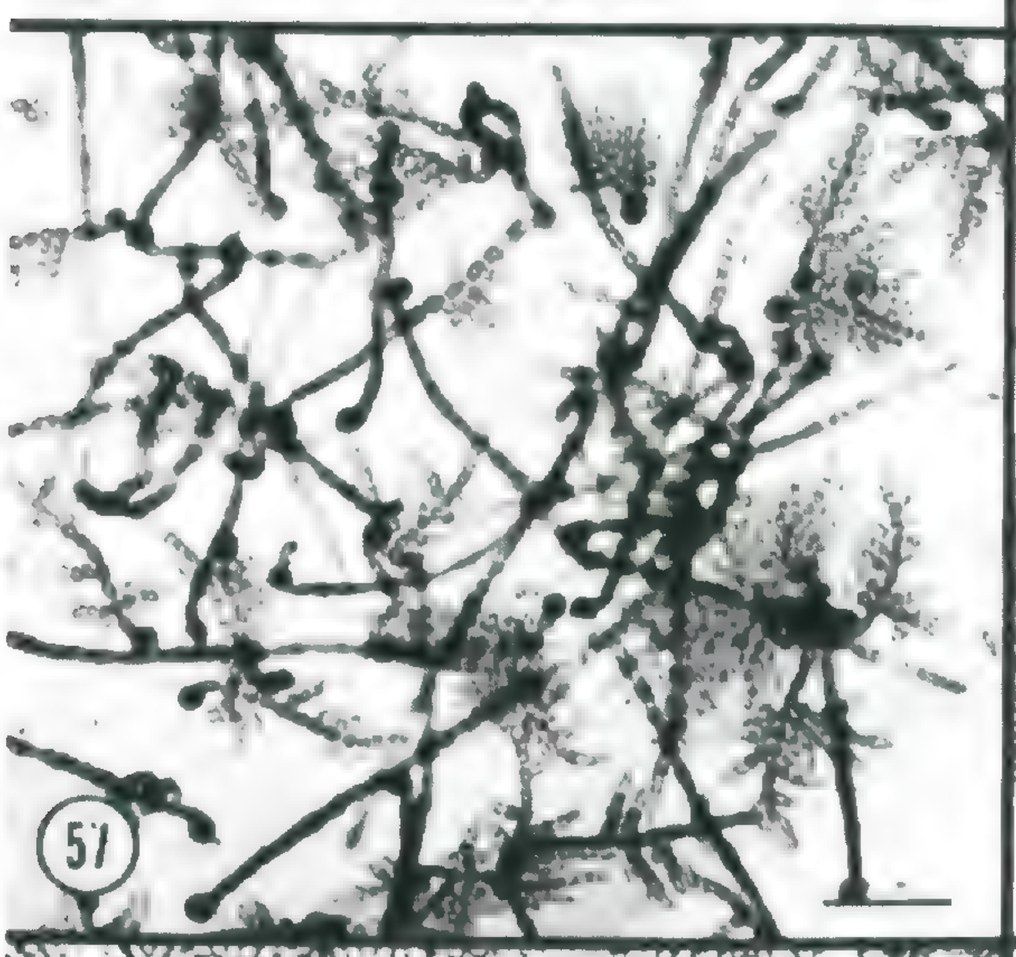

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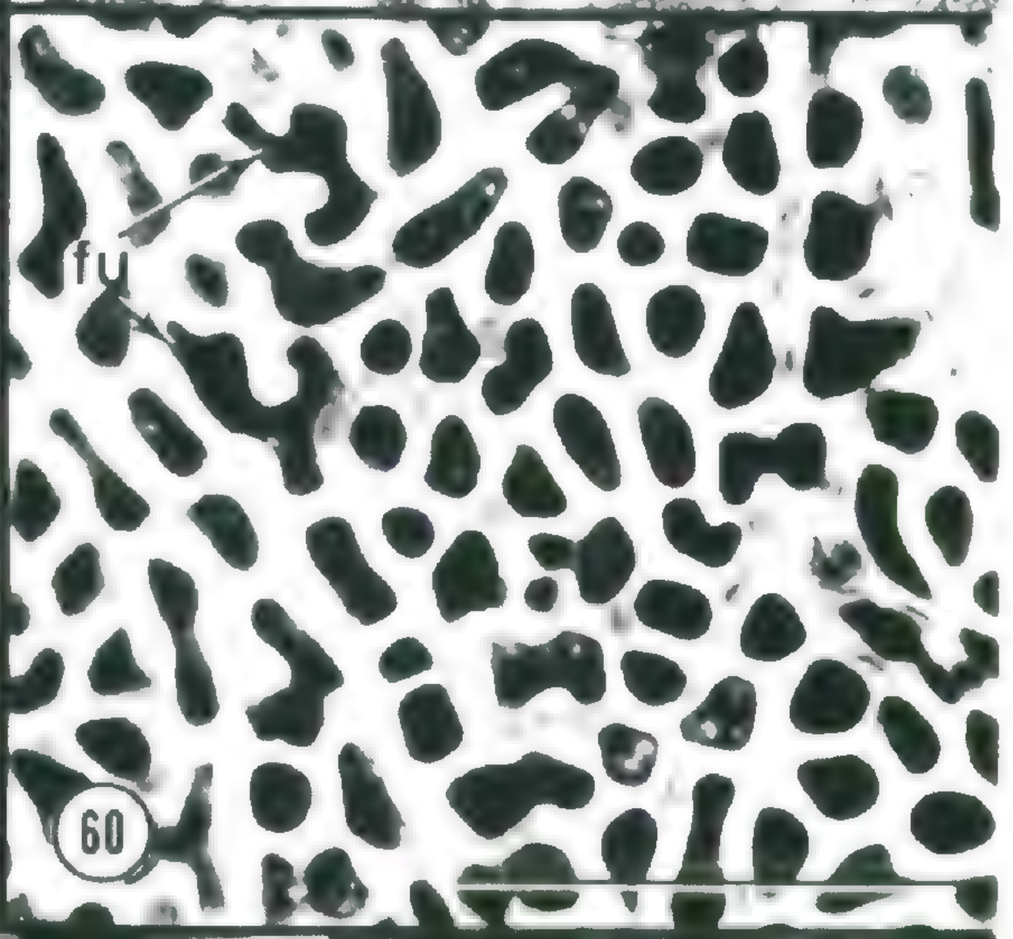

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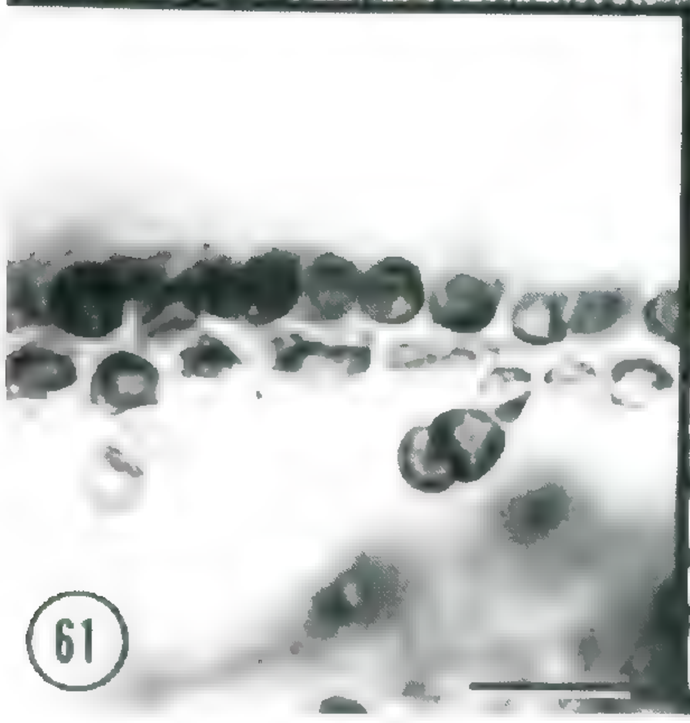

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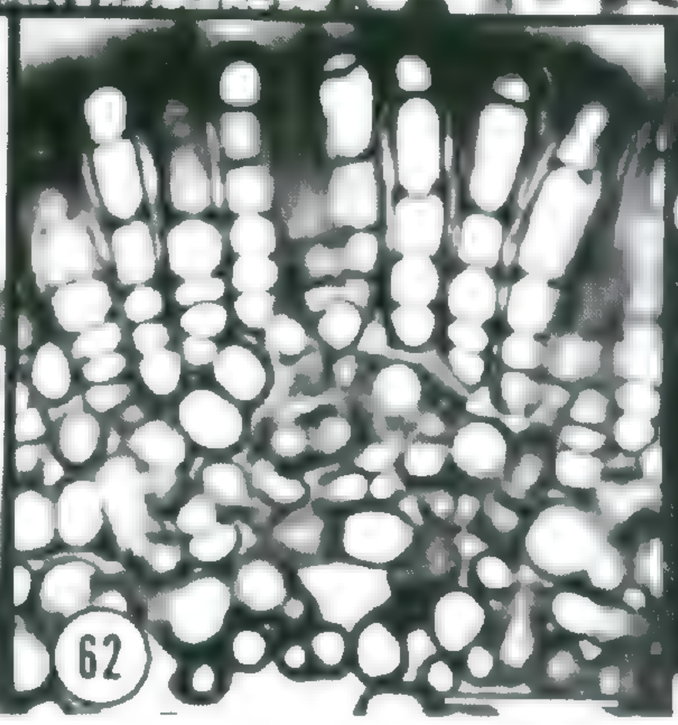

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of this genus. Cystocarpic rings in *C. carolinensis* are usually formed around a central cystocarp and are produced by the outward growth of gonimoblast filaments from it.

Using the terminology of Feldman (1952), the life history of *Cirrulicarpus carolinensis* may be considered to be digenetic, with an alternation of the gametophyte and carposporophyte generations. The absence of a tetrasporophyte generation in the life history can be explained if fertilization is not successfully achieved. The entire life history, including the development of the carposporophyte generation from vegetative cells, would then be haploid, and meiosis and tetraspore formation would be eliminated.

ACKNOWLEDGEMENTS

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Fig. 55–63. Growth of carpospores in culture.—55, a newly released spray of carpospores; scale, 200 μm.—56, carpospores germinating in unipolar (uni) and bipolar (bi) patterns; scale, 30 μm.—57, young germlings showing a heterotrichous pattern of development with branching prostrate filaments and unbranched upright filaments; scale, 50 μm. 58, a young crust similar in morphology to *Hymenoclonium serpens;* scale, 50 μm. 59, a maturing crustose phase with main axial filaments distinguishable by their elongated cell shape; scale, 50 μm. 60, cell fusions (fu) in the crustose phase; scale, 50 μm. 61, cross section through a distromatic area of the crust; scale, 20 μm.—62, cross section through a thickening with upright filaments; scale, 20 μm.—63, a young erect blade; scale, 1 cm.

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A COMPARISON OF THE SPECIES OF CIRRULICARPUS (KALLYMENIACEAE, RHODOPHYTA)

GAYLE I. HANSEN

ABSTRACT

The three known species of *Cirrulicarpus* have complanate, cartilaginous, repeatedly branched thalli which reach similar maximum heights. The plants are narrowly cuneate at their holdfasts and have apices which are broadly rounded or dichotomously or irregularly lobed. All the species have filamentous medullary systems and carpogonial branch apparati consisting of elongated or lobed cells. They differ in the number of carpogonial branches and subsidiary cells located on the supporting cell, the appearance and arrangement of cystocarps, the presence or absence of "giant cells" in the medulla, and in minor features of blade morphology.

INTRODUCTION

The genus *Cirrulicarpus* was established by Tokida and Masaki in 1956. The name refers to the characteristic ringed arrangement of the cystocarps on the surface of the fronds in the type species. The genus now includes the following three species: *C. gmelini* (Grunow) Tokida & Masaki from Hokkaido and the Aleutian Islands; *C. australis* Womersley & Norris from Port Phillip Heads in Australia; and *C. carolinensis* Hansen from the coast of North Carolina.

All three species of *Cirrulicarpus* have erect thalli that may reach 16 cm in height. The thalli are complanate, cartilaginous, and repeatedly branched in a subdichotomous manner, and they are attached to the substratum by a narrow holdfast. The blades have broadly rounded or irregularly lobed apices and margins that are entire or occasionally coarsely spinulose or erose. The genus resembles *Kallymenia* in having an essentially filamentous medullary system and a cortex of large inner cells grading into small outer cells. In species of *Cirrulicarpus*, the carpogonial branch systems consist of large, elongate or lobed supporting cells bearing three-celled carpogonial branches and subsidiary cells. The number of carpogonial branches and subsidiary cells present on a supporting cell varies with the species. Cells of the carpogonial branch apparatus are elongated and lobed and decrease in size from the supporting cell to the carpogonium. Cystocarps in all three species form in the upper portions of the fronds. The ring-like appearance of the cystocarps in *C. gmelini* is usually not evident in the other two species where cystocarps are generally solitary or in small irregular clusters. In section, cystocarps consist of numerous patches of carposporangia in chains separated by vegetative and gonimoblast filaments.

Cirrulicarpus gmelini (Grunow) Tokida & Masaki

When the genus *Cirrulicarpus* was first established, it included only *C. gmelini*. This species is based on *Kallymenia gmelini*, the name proposed by Grunow (1867) for a specimen collected in the Kurile Islands and deposited at the Botanisches Museum in Berlin–Dahlem. Grunow chose the specific epithet *gmelini* because the specimen resembled Gmelin's drawings (1768, pls. 22 and 23) of *Fucus palmetta*. Grunow included the species in *Kallymenia* because it is similar to other species of this genus in vegetative and reproductive structure. J. Agardh (1899) transferred Grunow's species to *Rhodymenia* without explanation. In 1915 Yendo transferred the species to *Erythrophyllum* because the vegetative structure of the thallus is similar to that of *E. delesserioides*, although thalli of *K. gmelini* lack the prominent midrib that occurs in *E. delesserioides*. Tokida and Masaki (1956) established the genus *Cirrulicarpus* for *K. gmelini* on the basis of reproductive characteristics. *Cirrulicarpus* differs from *Erythrophyllum* in having cystocarps located in rings (vs. in papillae) and intercalary tetrasporangia (vs. terminal). Norris, Tokida, and Masaki (1960) further studied the reproductive process in *C. gmelini* and confirmed *Cirrulicarpus* to be a distinct genus in the Kallymeniaceae.

Many reports have established the distribution of *Cirrulicarpus gmelini*. Okamura (1921) reported that it was common along the coast of Hokkaido. Nagai (1941) noted that it occurred only on the east coast of the northern and middle Kurile Islands. Setchell and Gardner (1903) found it off Agattu Island, Okamura (1933) off Atka Island, and recently Wynne (1970) off Amchitka Island, all islands in the Aleutians.

Vegetative Structure. *Cirrulicarpus gmelini* displays a subdichotomous to polychotomous branching pattern (Fig. 1). The plant is perennial, and older specimens have a thickened basal portion which is the previous year's growth. The older blades frequently become as narrow as 0.25 cm in width as a result of weathering and appear somewhat like an elongated portion of the stipe (Yendo, 1915). Dichotomies in older portions of the plant are usually acute and often appear torn while those in the younger portions are rounded. Apical bladelets formed during the most recent growing season are fan-shaped and irregularly dissected.

The cross-sectional anatomy of *Cirrulicarpus gmelini* is somewhat different from the other two species (Fig. 2). The outer cortical cells, though usually subglobose in shape, are often elongated anticlinally. The cells of the subcortex are ellipsoidal in shape and elongated periclinally. The medullary filaments consist of cells which vary from ellipsoidal to filiform in shape. Intermixed with these filaments are very large, irregularly elongated medullary cells which extend as filaments down from the apex and then irregularly throughout the thallus. These "giant cells," which are particularly prominent in female plants (Tokida &

Masaki, 1956), contain a "yellow homogeneous substance which is similar to the hyaline content of the carpogones of various red algae" (Yendo, 1915). These cells stain as intensely with aniline blue as do reproductive cells (Fig. 3). The occurrence of similar "giant cells" has been reported to occur in *Erythrophyllum delesserioides* and *Crossocarpus lamuticus* by Yendo.

Reproductive Structure. The carpogonial branch system of *Cirrulicarpus gmelini* was described by Norris, Tokida, and Masaki (1960) as consisting of one carpogonial branch of three cells, and two or three subsidiary cells on a large supporting cell. The cells are characteristically elongated and lobed (Fig. 5). During the development of the carpogonial branch, all of the cells, including the carpogonium with its trichogyne, are present before elongation and lobing of any of the cells occurs (Fig. 6).

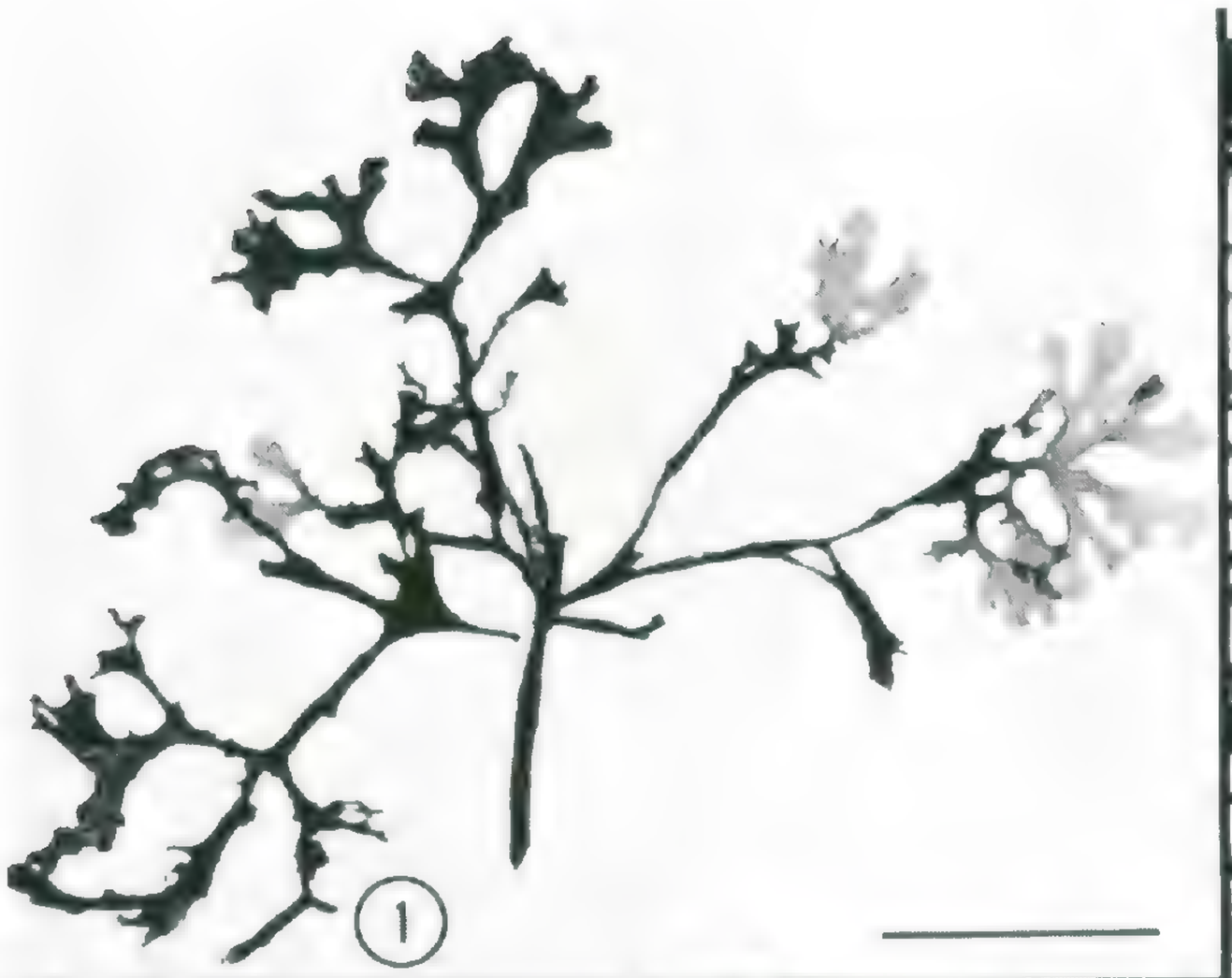
Post-fertilization processes in the alga were described as nonprocarpic by Norris *et al.*, (1960). After fertilization the carpogonium, supporting cell, and nearby subsidiary cells fuse. The large fusion cell is abundantly lobed and often appears connected to "giant cells" in the medulla (Fig. 7). According to Norris *et al.*, fusion cells form nonseptate connecting filaments which grow outward through the thallus and contact auxiliary cells which then form gonimoblast filaments with carposporangia at their apices. They suggest that the cystocarpic rings in this species are produced by a ring of auxiliary cells all of which are diploidized by connecting filaments from a central, fertilized, carpogonial branch system. Young post-fertilization stages other than fusion cells were not observed by these authors.

Cystocarps form in large patches on the upper portions of the fronds. Within the patches, groups of oval cystocarps, ranging from less than 0.1 to 1.0 mm in size, are arranged in elliptical and occasionally confluent rings (Fig. 4). Within cystocarpic areas, the thallus is considerably thickened but the cystocarps themselves raise the surface of the frond only slightly. In section, the cystocarps appear as clusters of carposporangia intermixed with vegetative and gonimoblast filaments (Fig. 8).

Tetrasporangial plants are similar to female plants in both habit and general morphology (Fig. 9). Tetrasporangia are abundant and scattered among the cortical cells as described by Yendo (1915). They are formed by direct conversion of cells one or two layers below the surface and thus are intercalary in origin (Tokida & Masaki, 1956). In Figs. 10 and 11 the upper or lower pit connections between tetrasporangia and nearby vegetative cells are clearly visible. The tetrasporangia are described by Tokida and Masaki as "obliquely cruciate in division."

Cirrulicarpus australis Womersley & Norris

A second species of *Cirrulicarpus*, *C. australis*, was established by Womersley and Norris (1971) for specimens from Port Phillip Heads,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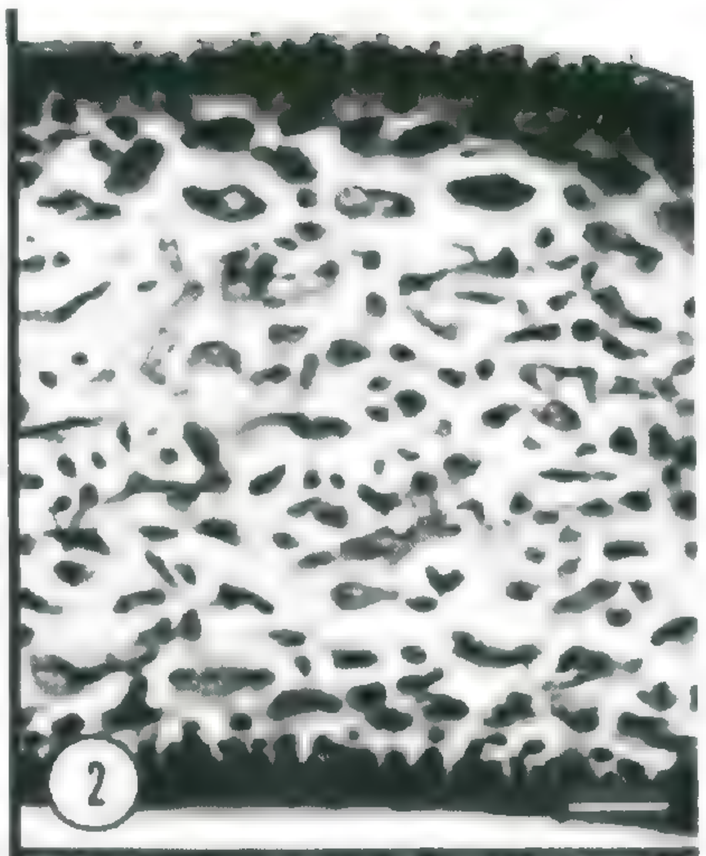
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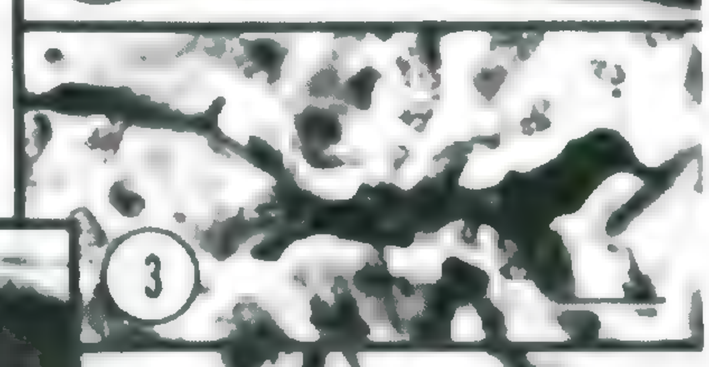
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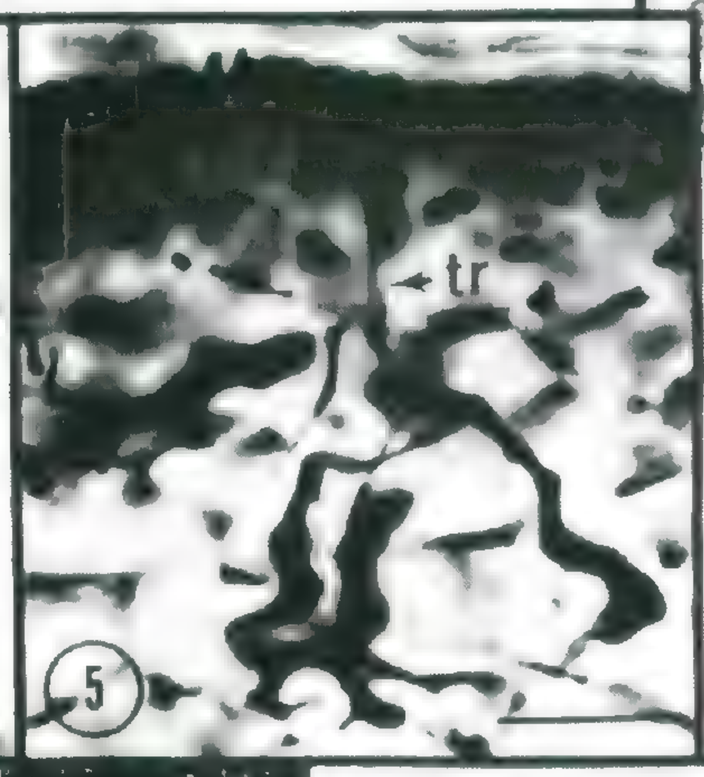
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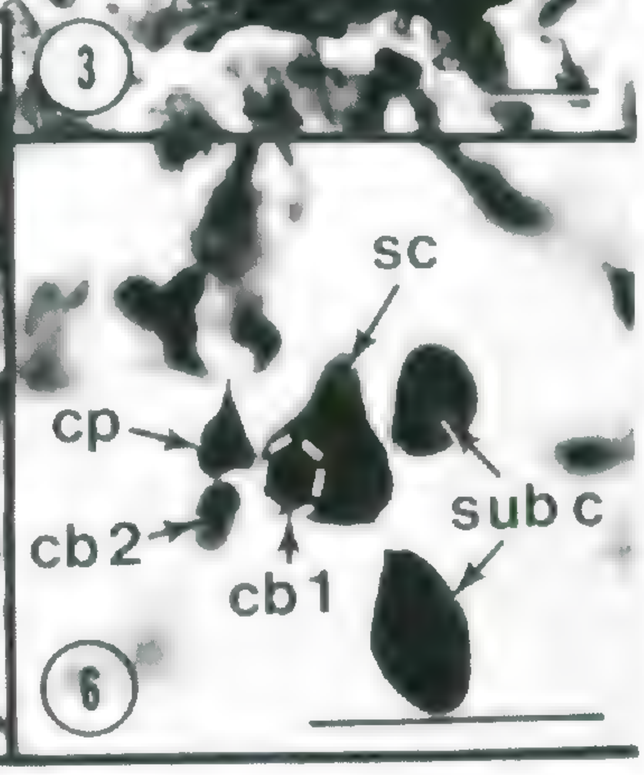
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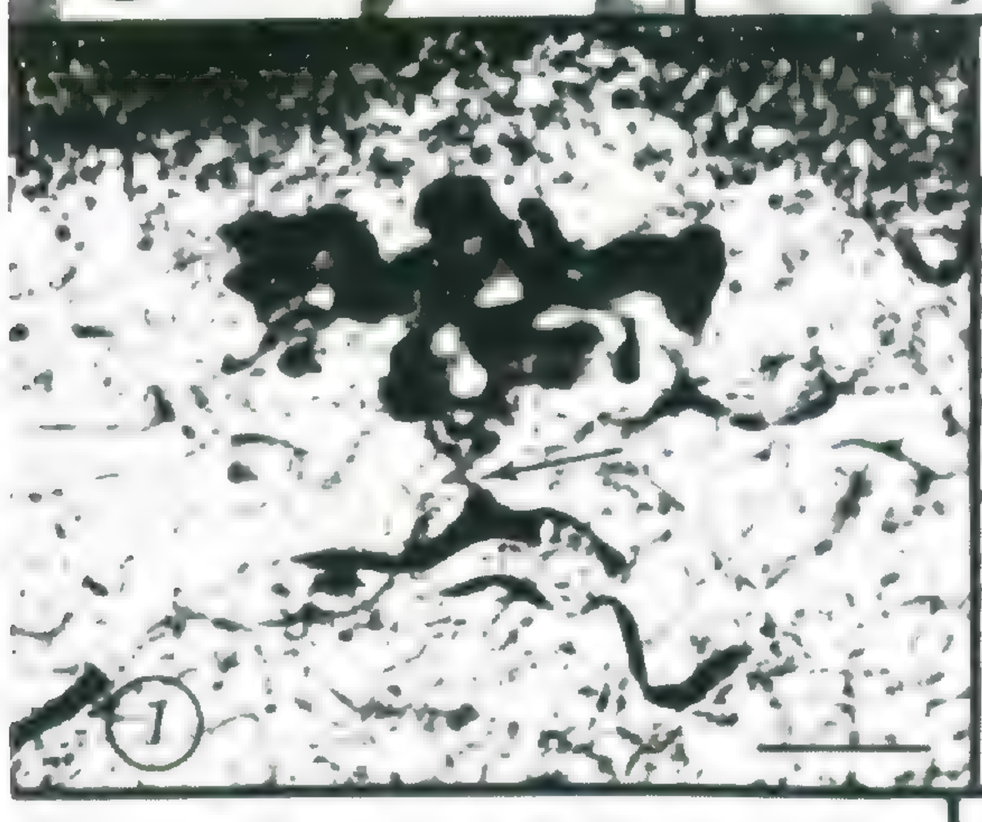
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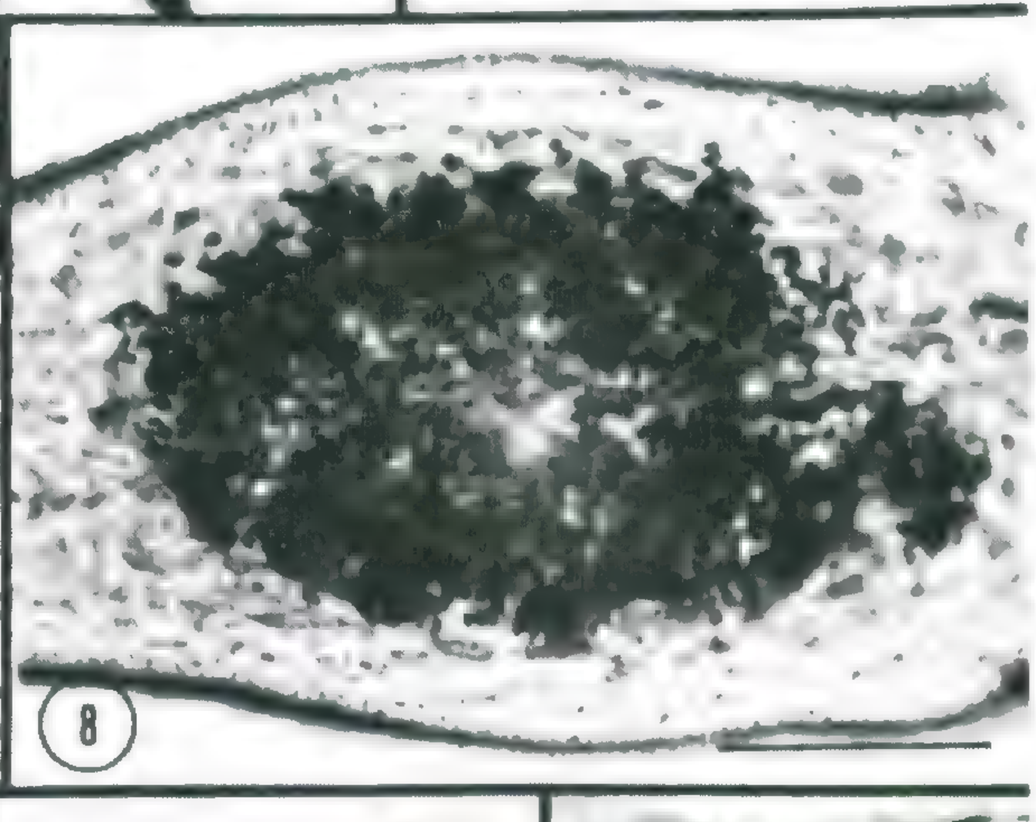
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Australia. These algae previously had been referred to *Cryptonemia inequalis*, a *nomen nudum* of Wilson (1892), or to *Kallymenia polycoelioides* J. Agardh, a different species recently redescribed by Womersley (1973). The authors put the species in *Cirrulicarpus* because the plants resembled *C. gmelini* in the cartilaginous and branched nature of the thallus and in the characteristic shape of the cells of the carpogonial branch system. Recently, Womersley (1973) has called *C. australis* and *Meredithia nana* synonyms; this is discussed on page 32.

Vegetative Structure. Plants of *Cirrulicarpus australis* are branched in a subdichotomous or occasionally polychotomous pattern as in other members of the genus (Fig. 12). However, in the specimens I have studied, no evidence of growth from a previous year is evident. There are no thickened basal portions and the dichotomies are always rounded and untorn. Thus the plant appears to be an annual even though individual plants are comparable in size and degree of branching to the other two species. Young branches of *C. australis* are usually narrower than those of the other species and often are about 0.5 cm in width. Due to these narrow upper branches, *C. australis* is usually less foliose in appearance than the other two species, which have broad apical bladelets. The apices of *C. australis* are uniformly rounded or variously lobed.

The cross sectional anatomy of *Cirrulicarpus australis* is essentially identical with that of *C. carolinensis* (Fig. 13). The outer cortex consists of subglobose cells which rarely appear elongated anticlinally. The subcortical cells are large and subglobose. The medulla consists of stellate cells that extend peridermally in a longitudinal direction in the thallus and filiform cells that extend in all directions.

Reproductive Structure. The carpogonial branch system in *Cirrulicarpus australis* differs from the other species in having up to five carpogonial branches. Five trichogynes are evident in Fig. 15. Womersley and Norris (1971) report that two to five carpogonial branches and up to six subsidiary cells may occur. The cells of the carpogonial branch system are similar in shape to those in the other two species though they frequently appear less broadly lobed. Early post-fertilization stages have not been observed in this alga. Womersley and Norris presumed that the female reproductive system was non-procarpic, as observed for *C. gmelini*,

FIG. 1–11. *Cirrulicarpus gmelini.*—1, female plant collected by Masaki on March 27, 1945, at Shireto-Misaki, Kushiro, Hokkaido; scale, 5 cm.—2, cross section of the blade; scale, 30 μm.—3, a large, deeply staining "giant cell"; scale, 30 μm.—4, fertile area with cystocarps grouped in rings; scale, 1 cm.—5, mature carpogonial branch system showing the elongated and lobed nature of the cells (tr = trichogyne); scale, 30 μm.—6, young carpogonial branch system in which the trichogyne has formed before the cells of the carpogonial branch have become elongated and lobed (cb 1, cb 2, cp = cells of the carpogonial branch, sc = supporting cell, sub c = subsidiary cell); scale, 30 μm.—7, fusion cell derived from cells of the carpogonial branch system with a pit connection (arrow) to a "giant cell" in the medulla; scale, 30 μm.—8, cross section through a mature cystocarp; scale, 30 μm.—9, tetrasporic plant collected by Masaki on November 30, 1955, at Shireto-Misaki; scale, 5 cm.—10, 11, sections showing the upper and lower pit connections (arrows) of the tetrasporangia (tsp); scale, 10 μm.

though they noted no fusion cells or connecting filaments. Short-celled filaments have been observed penetrating both reproductive and vegetative cells in this species as they do in *C. carolinensis*. In one specimen studied, a disintegrating carpogonial branch system had outward radiating filaments that appeared to be maturing into carposporangia (Fig. 16).

Cystocarps of *Cirrulicarpus australis* are scattered in small groups on the mid to upper portions of the fronds (Fig. 14). They are hemispherical and about 1 to 2 mm in diameter. When mature, the cystocarps push up the thallus surface more on one side than on the other, and they often become wart-like in appearance. The grouping of the cystocarps is irregular, and only occasionally are rings formed. When carpospores have been released from the central portion of a large cystocarp, a white central region or hole is formed giving the illusion of a ring of several confluent cystocarps; however, these structures actually develop from a single cystocarp. The same situation occurs in *C. carolinensis* (Fig. 54 of the previous paper). In section, cystocarps are composed of many clusters of carposporangia (Fig. 17) as seen in the other two species.

Though both male and tetrasporangial plants were reported as unknown by Womersley and Norris (1971), I found a tetrasporic specimen preserved in the Farlow Herbarium (Fig. 18). The specimen, identified as *Cryptonemia inequalis* J. Agardh, was collected by J. B. Wilson in 1895 from Port Phillip Heads. The plant is identical in habit and cross sectional anatomy to the female plants of *Cirrulicarpus australis*. Mature tetrasporangia are scattered among the cortical cells on both sides of the thallus. However, the tetrasporangia are not intercalary in origin: instead, they are formed from surface cortical cells which, during conversion to tetrasporangia, expand and sink below the surface leaving a vacant area in the cortex above them (Fig. 19). At times the wall of the sporangium is visible on the surface above the retracted, maturing tetrasporangium (Fig. 20). Tetraspores are cleaved from the parent sporangium in an imperfectly cruciate pattern.

Cirrulicarpus carolinensis Hansen

This species is described in detail in the previous paper, and thus it is discussed here only for comparative purposes.

Vegetative Structure. *Cirrulicarpus carolinensis* is widely foliose in habit, and branches in the typical subdichotomous pattern of species

FIG. 12–20. *Cirrulicarpus australis*.—12, holotype collected by J. B. Wilson on January 15, 1895, at Port Phillip Heads; scale, 3 cm.—13, cross section of the blade; scale, 100 μm.—14, fertile area showing the grouping and wart-like nature of the cystocarps; scale, 3 cm.—15, carpogonial branch system with five trichogynes (arrows); scale, 30 μm.—16, carpogonial branch systems with filaments radiating outward and forming what appear to be young carposporangia (arrow); scale, 100 μm.—17, cross section through a mature cystocarp, scale, 100 μm.—18, tetrasporic plant collected by J. B. Wilson on January 30, 1888, at Port Phillip Heads; scale, 3 cm.—19, section showing a sunken tetrasporangium cleaved in an irregularly cruciate fashion; scale, 10 μm.—20, section with tetrasporangium retracted below the surface leaving behind the empty wall; scale, 10 μm.

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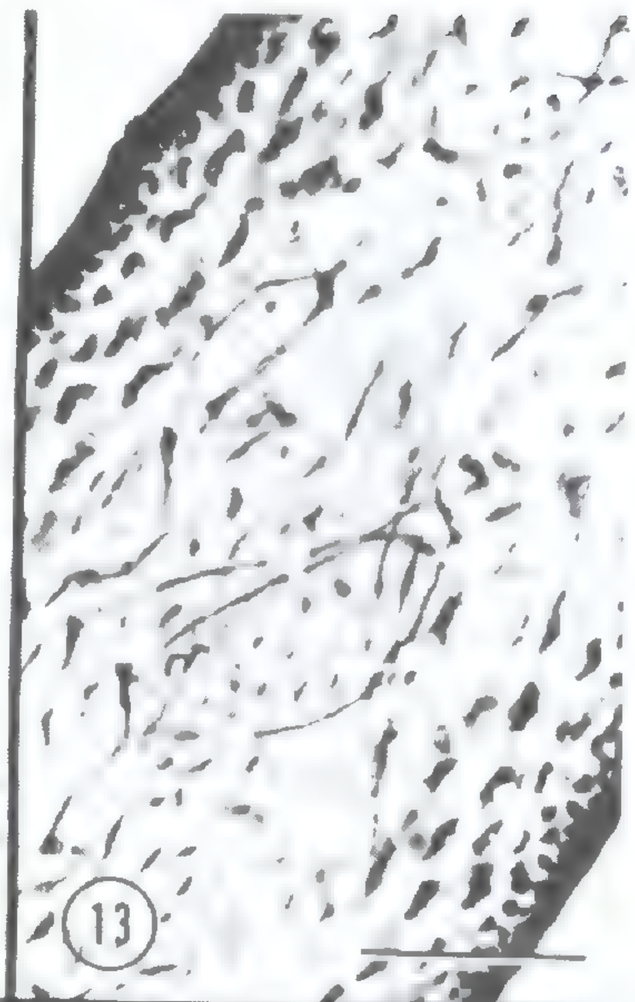
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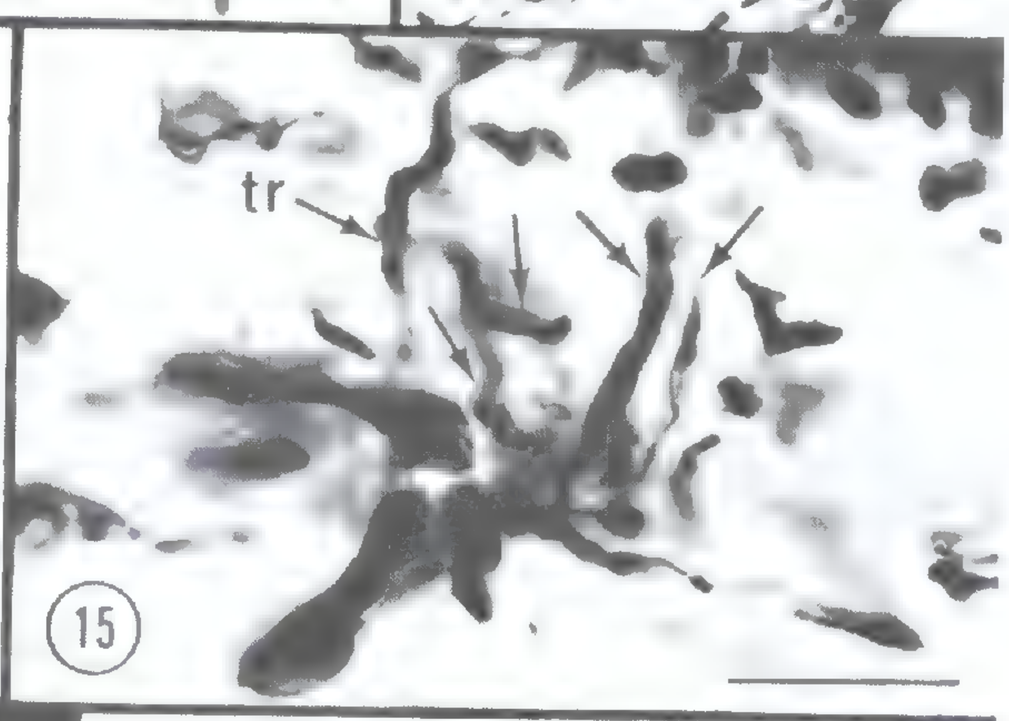

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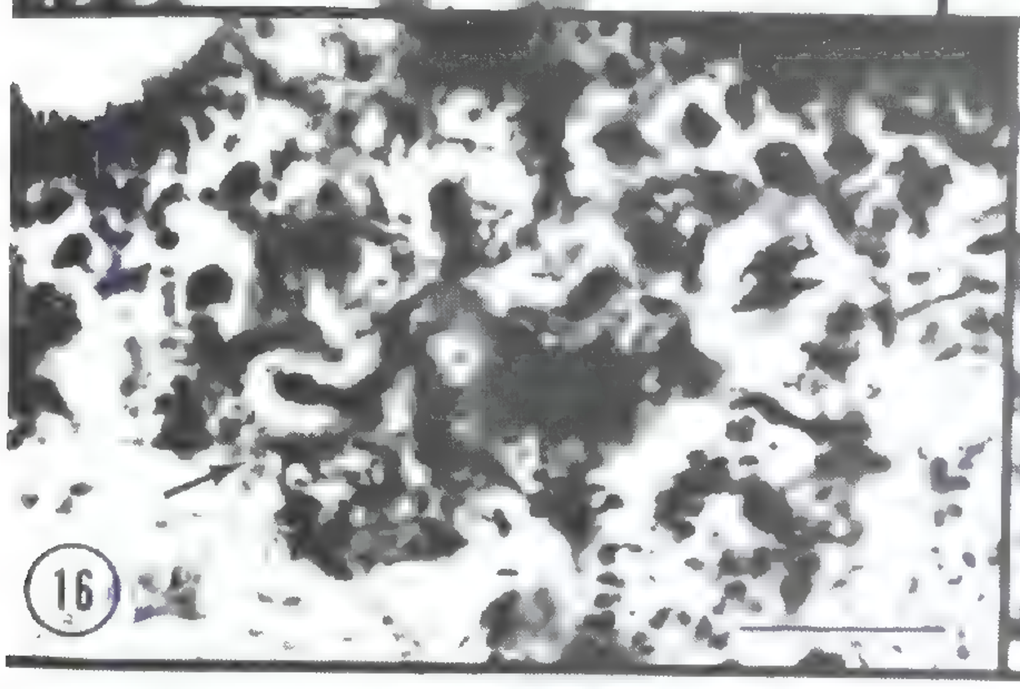
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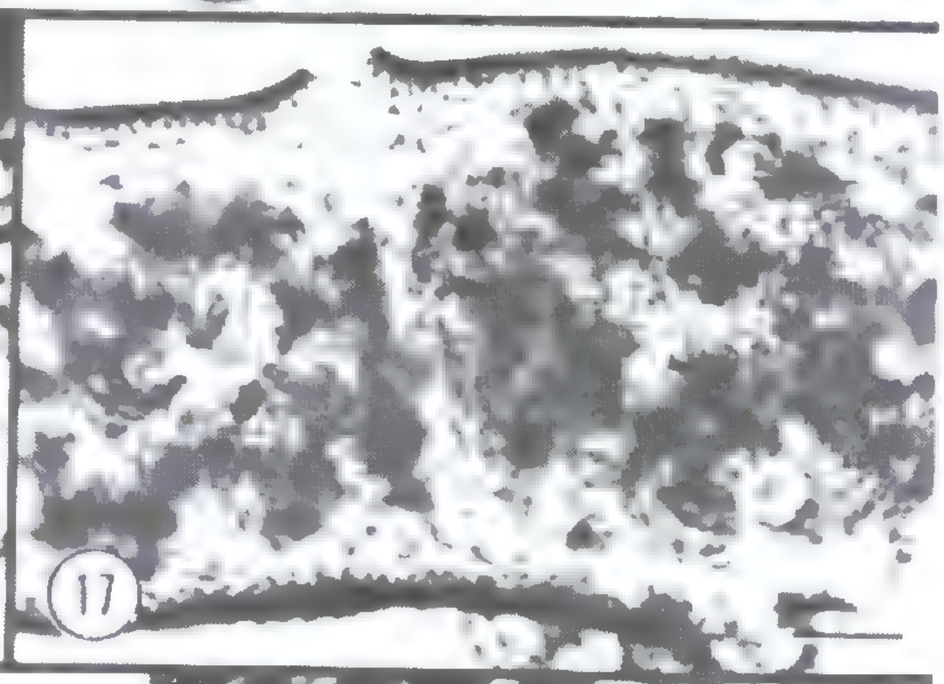
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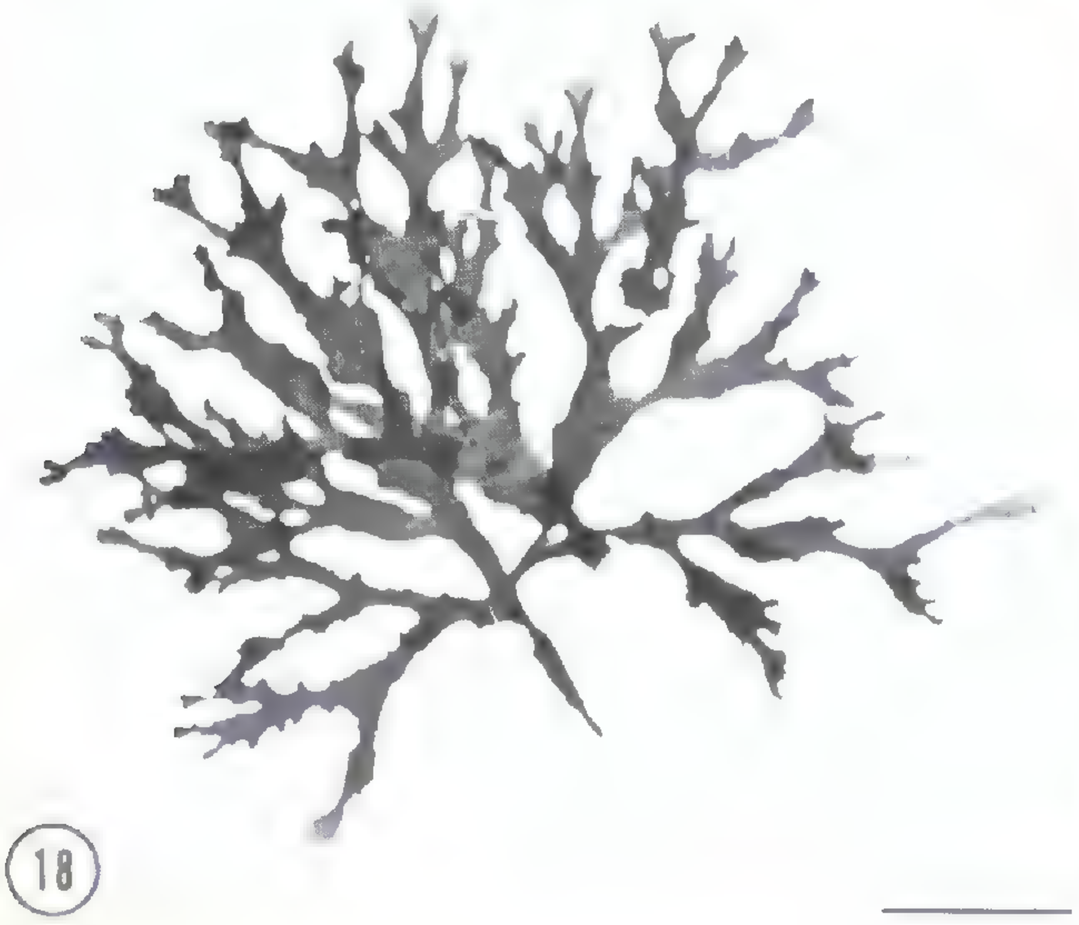
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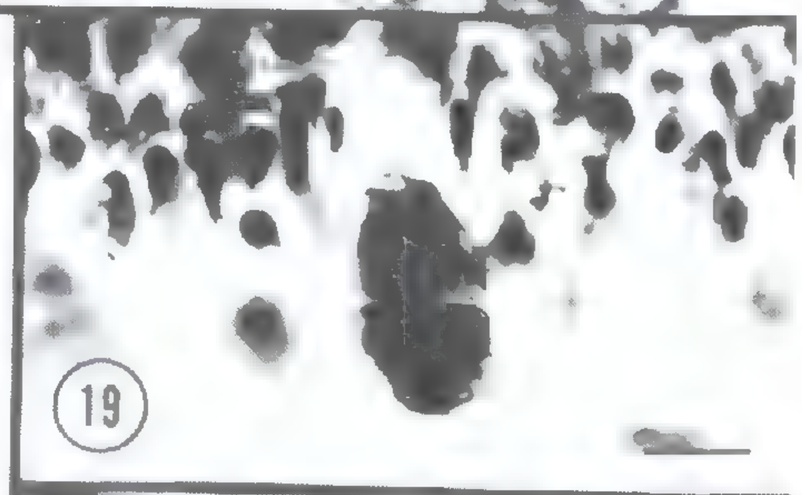
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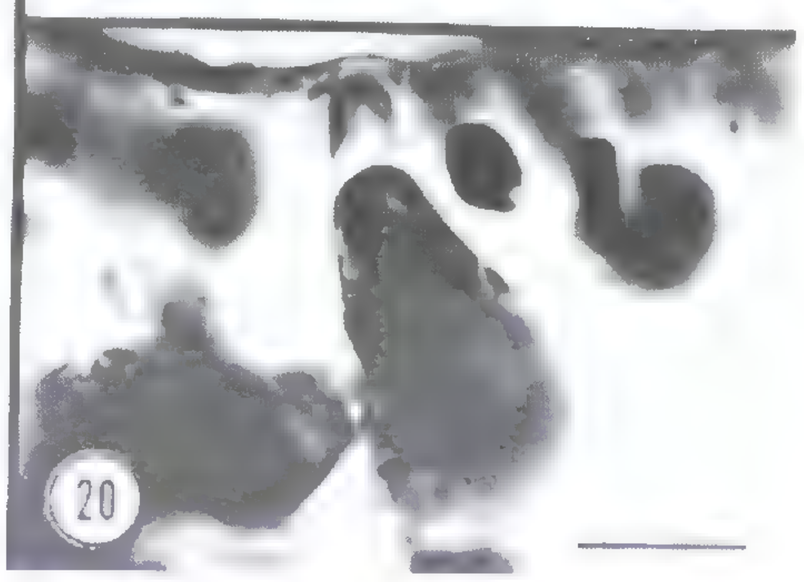
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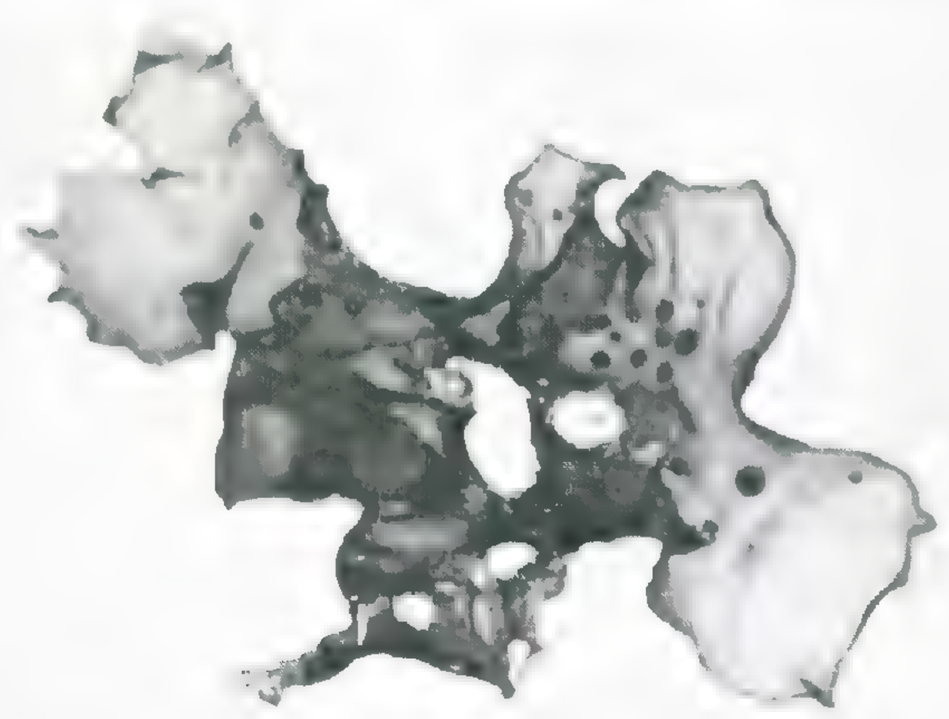
in this genus. Because the plant is perennial like *C. gmelíni*, the older dichotomies are acute and show evidence of tearing, while the younger ones are rounded. Older portions of the thalli become thickened and worn from weathering, though they never become as narrow as the stipe-like older blades of *C. gmelini*. Young apical bladelets in *C. carolinensis* are obovate-lobed and easily distinguish the plant from *C. gmelini* which has fan-shaped apical bladelets.

The cross sectional anatomy of *Cirrulicarpus carolinensis* consists of a medulla of stellate and filiform cells and a cortex of large subglobose cells that grade into smaller nearly globose outer cells very much like those of *C. australis*. "Giant cells" never occur in the medulla of this species.

Reproductive Structure. The carpogonial branch system of *Cirruli-*



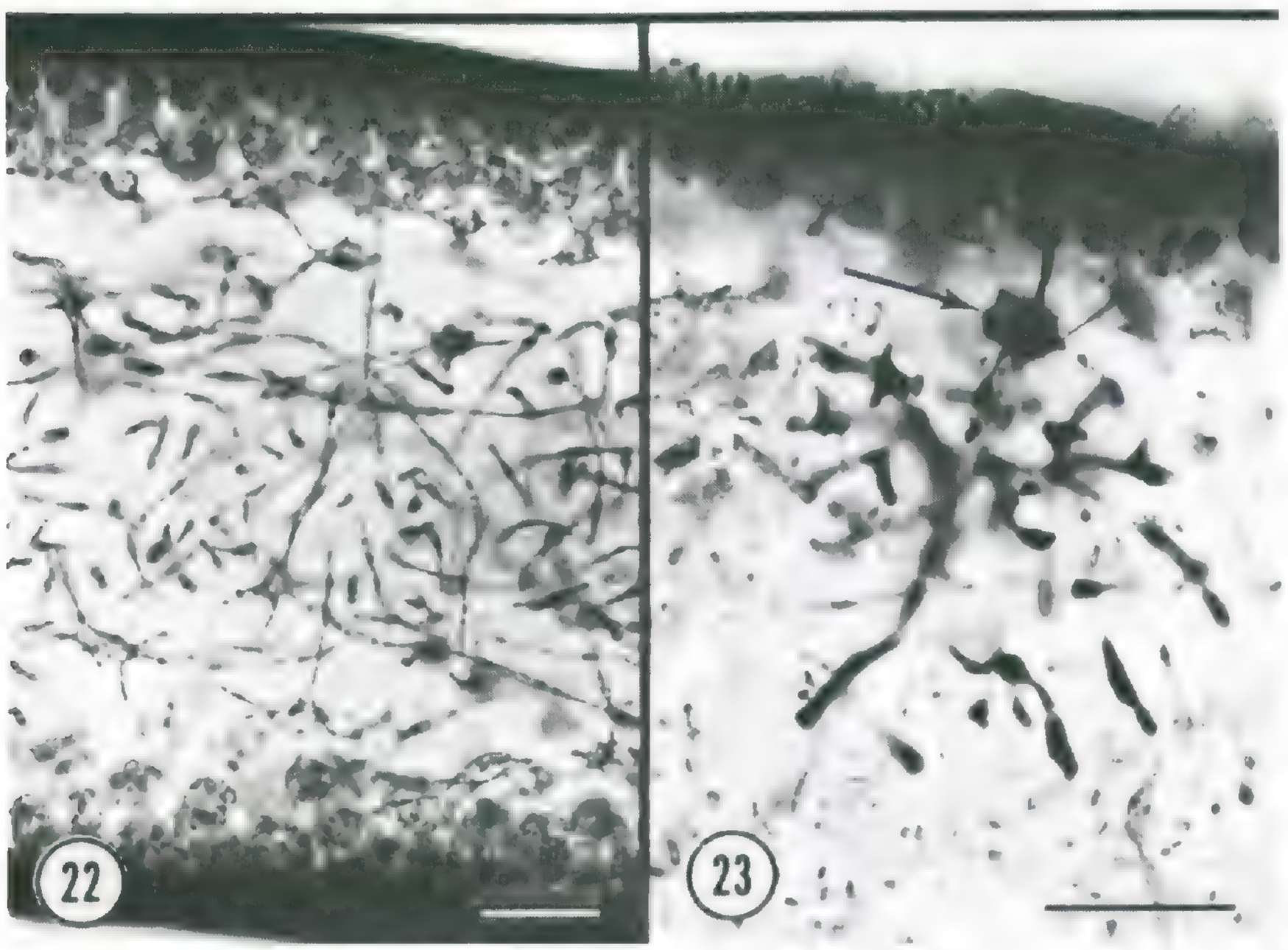


FIG. 21–23. *Meredithia nana*.—21, lectotype collected by J. B. Wilson on January 27, 1883 at Port Phillip Heads; scale, 1 cm.—22, cross section of the blade; scale, 50 μm.—23, section showing gonimoblast development from a cell (arrow) which appears to be vegetative in nature; scale, 50 μm.

carpus carolinensis consists of one or two carpogonial branches of three cells, and occasionally one or two subsidiary cells on the lobed supporting cell. The branch system resembles that of *C. gmelini* which consistently has only one carpogonial branch. During development, the cells of the carpogonial branch apparatus elongate and lobe before the formation of the carpogonium—unlike the development of the branch apparatus in *C. gmelini.*

Development of the carposporophyte in *Cirrulicarpus carolinensis* is unique in the genus. Gonimoblast filaments are produced from vegetative cells and frequently can be seen penetrating and digesting both vegetative and reproductive cells before forming carposporangia. Cystocarps occasionally form in rings. However, the rings are caused by the outward growth of secondary gonimoblast filaments from the central cystocarp and not by the outward growth of primary gonimoblast or connecting filaments to auxiliary cells as is reported to occur in *C. gmelini* (Norris, *et al.*, 1960).

No tetrasporophyte generation is present in *Cirrulicarpus carolinensis.* The alga is able to bypass this stage in its life history and forms erect gametophytic blades directly from carpospore germlings. The occurrence or lack of a tetrasporophytic generation among the species of one genus is not a serious taxonomic problem. Martin (1969) has pointed out that variations of this kind occur in the life histories of numerous red algae and may, at times, even be caused by environmental factors.

DISCUSSION

The genus *Cirrulicarpus* comprises a group of species within the Kallymeniaceae that are cartilaginous and complanate, have repeatedly branched thalli, filamentous medullary systems, and carpogonial branch systems consisting of elongated or lobed cells. Womersley and Norris (1971) considered the divided nature of the blades an important characteristic for distinguishing *Cirrulicarpus* from *Kallymenia.* Womersley (1973) also pointed out that the cartilaginous texture of *Cirrulicarpus* distinguishes it from the softer *Kallymenia.* Species of *Cirrulicarpus* differ from one another in the characters outlined in Table 1. The most important characters differentiating the species appear to be the number of branches in the carpogonial branch systems, the presence or lack of "giant cells" in the medulla, and the appearance and arrangement of the cystocarps.

Norris, *et al.*, (1960) suggested that *Cirrulicarpus gmelini* was a primitive member of the Kallymeniaceae because it had a filamentous medullary system and because it bore carpogonial branches on its auxiliary cell system. Auxiliary cell systems have not been seen in all species of *Cirrulicarpus*, but all do have filamentous medullary systems. Norris (1957) also established that within the Kallymeniaceae, species with fewer carpo-

TABLE 1. A COMPARISON OF THE SPECIES OF CIRRULICARPUS

	C. gmelini	C. australis	C. carolinensis
Apical bladelets or branches	Fan-shaped, irregularly dissected	Narrow, dichotomously or polychotomously lobed	Obovate, broadly rounded or dichotomously lobed
Branching in mature blades	Subdichotomous-acute	Subdichotomous-rounded	Subdichotomous-acute
Growth	Perennial	Annual	Perennial
Medullary cells	Filiform to ellipsoidal cells; "giant cells" present	Filiform and stellate cells; "giant cells" absent	Filiform and stellate cells; "giant cells" absent
Carpogonial branch systems	1 carpogonial branch, 2–3 subsidiary cells	2–5 carpogonial branches, 0–6 subsidiary cells	1–2 carpogonial branches, 0–2 subsidiary cells
Cystocarp arrangement	Clusters, usually in small elliptical rings	Solitary, in clusters, rarely in rings	Solitary, in clusters, rarely in rings
Male gametophytes	Unknown	Unknown	Present
Tetrasporophytes	Present, tetra-sporangia intercalary	Present, tetraspor-angia terminal	Absent
Distribution	Hokkaido, Kurile and Aleutian Islands	Port Phillip Heads, Victoria, Australia	North Carolina

gonial branches on their supporting cells are more advanced. Thus *C. australis* with two to five carpogonial branches can be considered the most primitive, *C. carolinensis* with one or two carpogonial branches intermediate, and *C. gmelini* with only one branch, the most advanced.

The disjunct distribution of the species of *Cirrulicarpus* presents a problem. It is difficult to believe that species so widely separated geographically could share a common ancestor. However, as the marine algal flora of the intermediate localities is more thoroughly investigated, additional species of *Cirrulicarpus* may be discovered that better link the three established species.

EXCLUDED SPECIES

Meredithia nana J. Agardh

In 1973 Womersley transferred *Meredithia nana* J. Agardh (1892) to *Cirrulicarpus* making the new combination *Cirrulicarpus nana*. He considered the type specimen of *M. nana* to be a young frond of *C. australis*, and therefore placed *C. australis* in synonymy under *C. nana*. Earlier Womersley and Norris (1971) had expressed doubt as to whether *M. nana* was a member of the Kallymeniaceae due to the different nature of the carpogonial branch system and suggested that it might be a

member of the Gigartinales. In proposing the transfer, Womersley stated that the identical vegetative structure of the plants in cross section and the similarity of their type localities were sufficient evidence of the synonymy of the two species.

I have studied several specimens of *Meredithia nana* J. Agardh, including the lectotype (Fig. 21), which is cystocarpic. The cross sectional anatomy of the plant (Fig. 22) is similar to both *Cirrulicarpus australis* and *C. carolinensis*. Although the carpogonial branch systems in *M. nana* have not been observed in a young enough state to describe precisely, they do appear to differ from those of *C. australis*. Post-fertilization stages have been observed, and gonimoblast filaments appear to develop from an auxiliary cell which is vegetative in nature (Fig. 23). This indicates that *M. nana* is most likely a member of the Gigartinales, as originally suggested by Womersley and Norris, and that it is not a member of the genus *Cirrulicarpus*.

ACKNOWLEDGEMENTS

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Herbarium specimens of *Cirrulicarpus australis*, *C. carolinensis*, *C. gmelini*, and *Meredithia nana* were generously loaned by the following institutions and individuals: Duke University (DUKE), Farlow Herbarium of Harvard University (FH), Botanical Museum at Lund (LD), National Herbarium of Victoria (MEL), University of North Carolina (NCU), University of California at Berkeley (UC), U.S. National Museum (US), Dr. G. Kraft, University of Melbourne, Australia, Dr. T. Masaki, Hokkaido University, Japan, and Dr. C. Schneider, Trinity College, Connecticut.

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STUDIES IN CRYPHAEACEAE III. SPHAEROTHECIELLA FLEISCH. NEW TO THE AMERICAS[1]

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ABSTRACT

The genus *Sphaerotheciella* Fleisch., previously known from eastern Asia, is reported new to the neotropics (Mexico and Venezuela). The combination S. *pinnata* (B.S.G.) Manuel is made. *Cryphaea corrugata* Card. and *Pilotrichum decurrens* C. Müll. are conspecific with S. *pinnata*. All names are lectotypified. The presence of endosporic germination and intrathecial protonemata in *Sphaerotheciella* is discussed.

INTRODUCTION

Bryophytes (and vascular plants) having a disjunct distribution between eastern Asia and northern Latin America are rather well-known (Sharp, 1953 & 1972; Sharp & Iwatsuki, 1965; Wood, 1972). It is therefore not phytogeographically surprising to find the genus *Sphaerotheciella* Fleisch. in the bryoflora of northern Latin America. It is known otherwise from a single species (S. *sphaerocarpa* (Hook.) Fleisch.) found in Nepal, Sikkim, Bhutan, and southern China (Szechwan and Yunnan) (Noguchi, 1966 & 1971). A second species is herein added to the genus by the transfer of *Cryphaea pinnata* B.S.G. This taxon has been recognized since 1850. *Sphaerotheciella pinnata* (B.S.G.) Manuel occurs in Mexico and Venezuela and is very likely to be found in Central America (Fig. 1).

MORPHOLOGICAL NOTES

Sphaerotheciella Fleisch. is distinguished from the other six genera of the Cryphaeaceae in having erect gametophores, short lateral perichaetial branches, globose thecae, double peristomes, and endosporic germination associated with precocious intrathecial protonemal development. Although endosporic germination is known to occur in several other genera of "true mosses" e.g., *Dicnemon* Schwaegr., *Encamptodon* Mont., *Mesotus* Mitt. *in* Hook., and *Cleistostoma* Brid. (Ruhland, 1925), it is considered rare. However, such protonemata are rather common in Hepatophytina particularly in the orders Jungermanniales and Metzgeriales.

Nehira (1966 & 1974) recognized three basic groups for 18 different sporeling patterns in the Jungermanniales. "Group III" consists of protonemata that form inside enlarged exospores. From my preliminary observations the pattern of sporeling development in S. *pinnata* seems to coincide with *Radula* type of Group III, *viz.* "spore germination occurs inside the enlarged exospore and a usually unistratose, multicellular,

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disk-like protonema is formed through intercalary divisions" (Nehira, 1974, p. 157). Further studies are underway to clarify the pattern of sporeling development in *Sphaerotheciella*.

SYSTEMATIC TREATMENT

KEY TO THE SPECIES

Leaf apices acuminate to somewhat abruptly contracted into wide, short, irregularly denticulate acumina; costae 0.75–0.88 the length of leaves .... S. *pinnata* (B.S.G.) Manuel.

Leaf apices acuminate to abruptly contracted into narrow acumina, acumina short to long, entire, rarely denticulate; costae 0.5–0.6(–0.7) the length of leaves .... S. *sphaerocarpa* (Hook.) Fleisch.

Sphaerotheciella pinnata (B.S.G.) Manuel, comb. nov.

FIGS. 2–10

Basionym, *Cryphaea pinnata* B.S.G., Bryol. Eur. **5**:35. 1850 (fasc. 44–45, mon. 5). *Vide* nomen, remark 1.

Pilotrichum decurrens C. Müll., Syn. Musc. **2**:172. 1851 (*syn. nov.*).–*Cryphaea decurrens* (C. Müll.) Mitt., Jour. Linn. Soc., Bot. **12**:414. 1869.–*Cryphaea patens* var. *decurrens* (C. Müll.) Schimp. *ex* Par., Index Bryol. 290. 1894.–*Cryphaea patens* var. *decurrens* (C. Müll.) Schimp. & Par. *ex* Par. *ex* Wijk *et al.*, Index Musc. **1**:517. 1959 (*err. cit.*). TYPE: Mexico. S. *loc., Ehrenberg, s.n.* (lectotype: BM!). *Vide* nomen, remark 2.

Cryphaea corrugata Card., Rev. Bryol. **38**:39. 1911 (*syn. nov.*). TYPE: Mexico. Etat de Puebla. Esperanza, *Purpus 4294* (lectotype: S–PA!; isotype: PC?). *Vide* nomen, remark 3.

Gametophores green to dark green. Stoloniform shoots creeping, generally inconspicuous; stems erect, up to 7 cm tall, pimately to irregularly pimately branched; branches 0.5–2.0 cm long. Flagelliform branches not observed. Stem leaves imbricate to loosely imbricate, occasionally

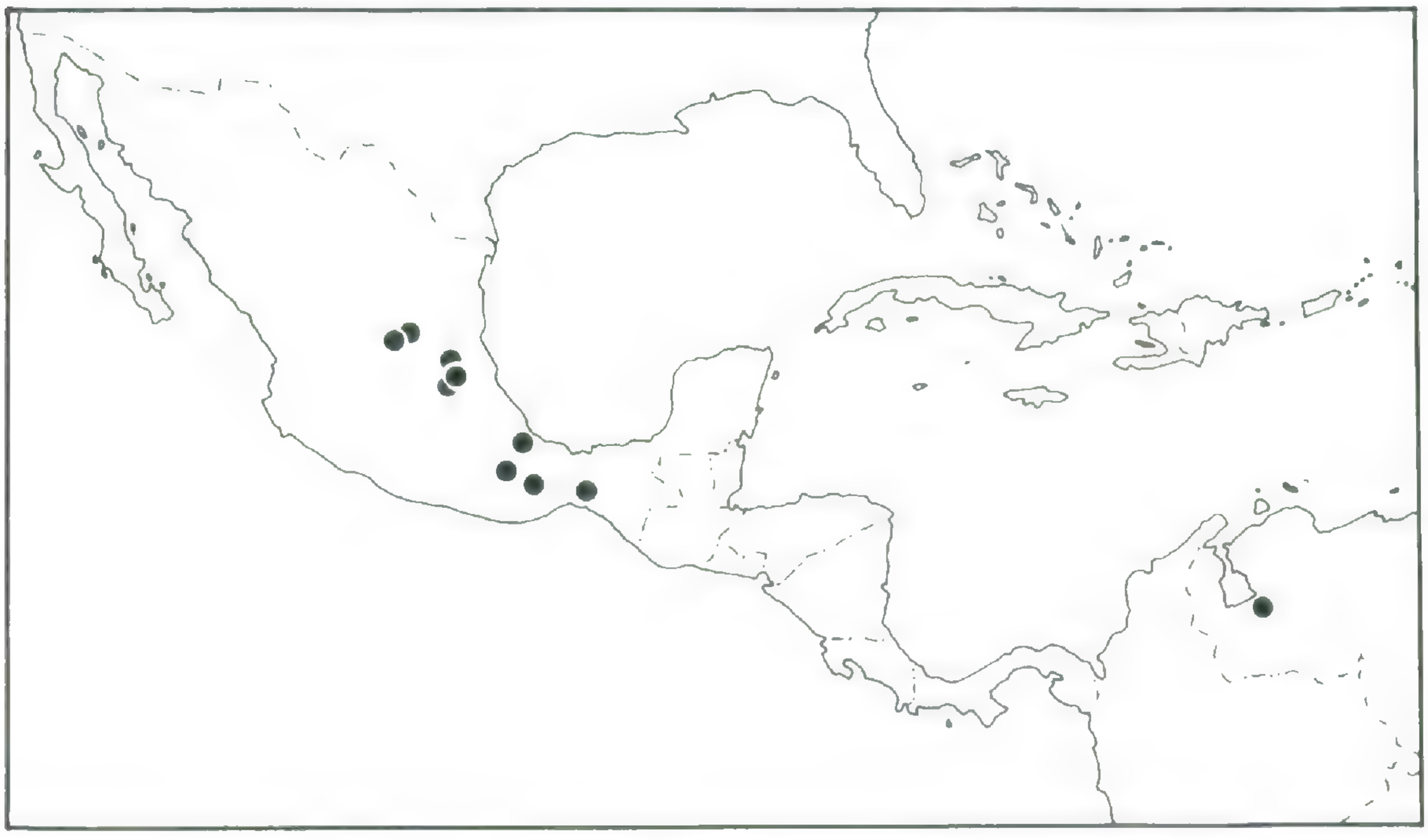

FIG. 1. Distribution map of *Sphaerotheciella pinnata*.

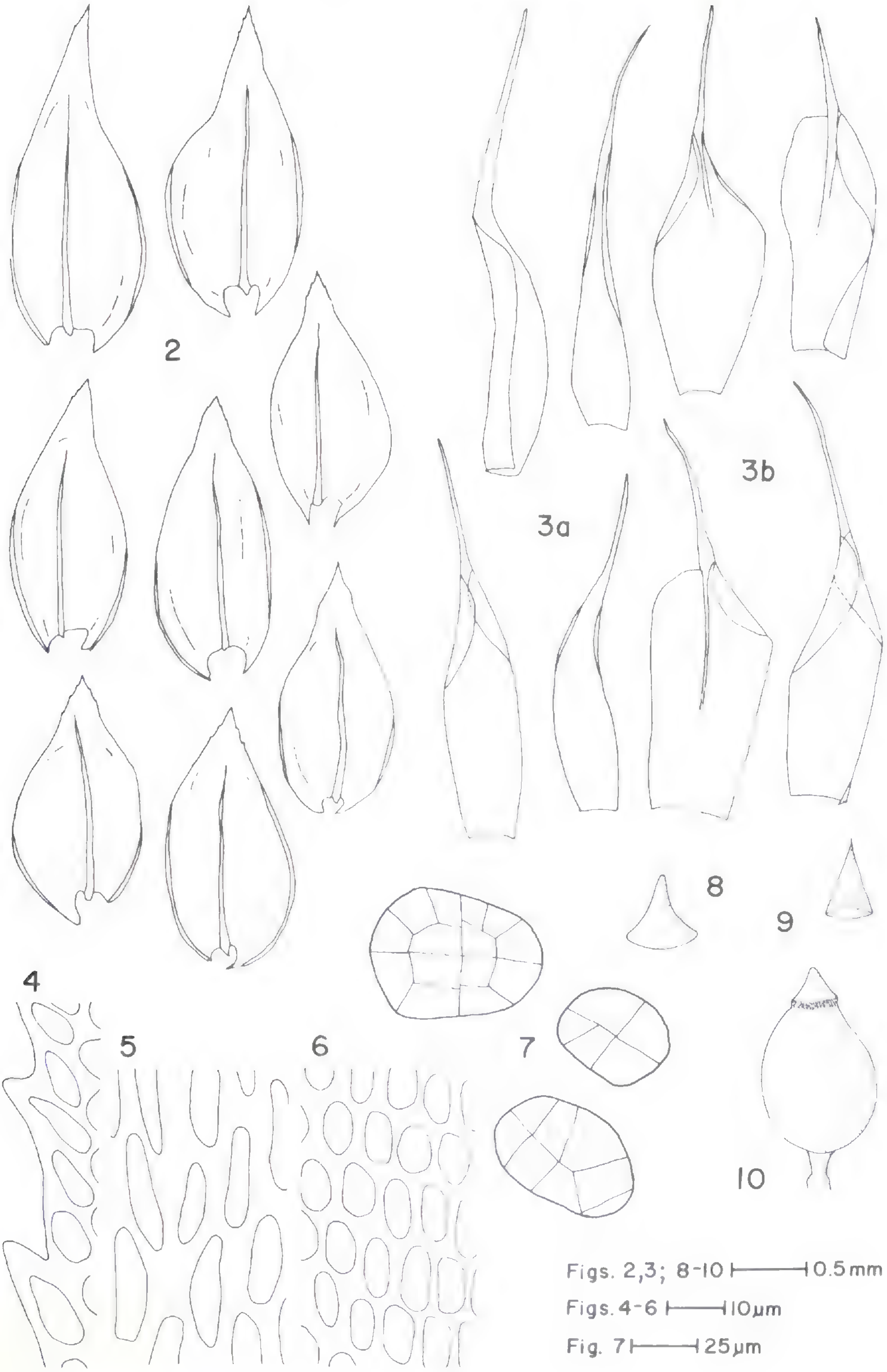

FIG. 2–10. *Sphaerotheciella pinnata:*—2. leaves.—3a. outer perichaetial leaves.—3b. inner perichaetial leaves.—4. apical margin of leaf.—5. apical cells of leaf.—6. medial cells of leaf.—7. protonemata.—8. operculum.—9. calyptra.—10. theca.

wrinkled when dry, spreading when wet, ovate-lanceolate, concave, (0.4–)0.6–0.9(–1.0) × (1.0–)1.2–1.8(–2.4) mm; apices acuminate to somewhat abruptly contracted into wide, short acumina; bases decurrent; margins revolute proximally to 0.50–0.75 the length of leaves, plane and irregularly denticulate at apices, entire below; unicostate, costae 0.75–0.88 the length of leaves, 30.8–61.6 μm wide at bases; cells thick-walled, smooth; basal marginal cells quardrate to transversely oval; inner basal cells fusiform; medial cells narrowly elliptic to widely elliptic, 4.4–11.0 (–13.0) × (5.8–)11.0–17.6 μm; apical cells narrowly elliptic to fusiform, 5.5–13.2 × 13.2–24.2(–26.4) μm. Branch leaves similar to stem leaves except smaller and less denticulate. Autoicious. Perigonal bracts ovate to ovate-lanceolate, 0.2–0.3 × 0.45–0.6(–0.8) mm; apices acuminate; generally ecostate; cells smooth. Outer perichaetial bracts ovate to lanceolate, 0.4–0.7(–1.0) × 2.0–3.0 mm; apices acuminate to abruptly acuminate into long, smooth awns; margins plane to revolute, entire; unicostate, costae percurrent to excurrent; cells smooth. Inner perichaetial bracts obovate, 0.4–0.7(–0.9) × 2.3–3.5 mm; apices abruptly contracted into long, smooth awns; shoulders sometimes revolute; margins entire throughout or occasionally slightly serrulate at shoulders; unicostate, costae excurrent into long awns.

Spore germination endosporic, protonemata intrathecial, thalloid, 30–66 × 44.0–96.8 μm.

Thecae globose to widely obovate, (0.6–)0.7–1.0(–1.1) × 0.9–1.3(–1.5) mm; stomata not observed; exostome teeth narrowly lanceolate, smooth, proximally, papillose distally, 0.4–0.58 mm long; endostome segments rudimentary, smooth, ca 0.25 mm long; cilia none; annuli compound; opercula conic, 0.3–0.5 × 0.4–0.5 mm.

Calyptrae mitrate, smooth, 0.2–0.4 × 0.5–0.6 mm.

Type. Mexico. *S. loc., Liebmann, s.n.* (lectotype: BM!).

Habitat. Corticolous or ramicolous on trees and shrubs between 1700 and 3100 meters.

Distribution. Mexico and Venezuela.

Nomenclatural Remarks. 1. Only a single specimen could be found which matched the scant information contained in the protologue of *Cryphaea pinnata* B.S.G. This specimen, herein designated lectotype, is in the British Museum. It was formerly in the herbarium of T. Gümbel, one of the three publishing authors.

2. Carl Müller's types were destroyed during World War II. Thus, the name *Pilotrichum decurrens* needs lectotypification. From among the several specimens examined which were collected in Mexico by Ehrenberg, I have designated a specimen in the British Museum to serve as lectotype.

3. Cardot (1911) failed to mention a holotype in the protologue of *Cryphaea corrugata*. Accordingly I have designated the isotype at S–PA

a lectotype. Presumably an isotype also exists in Cardot's herbarium at PC.

Taxonomic Remarks. 1. *Cryphaea corrugata* Card., *C. pinnata* B.S.G. and *Pilotrichum decurrens* C. Müll. are based upon differences in leaf size, shape of leaf apices, costal lengths, and the degree to which the leaves are wrinkled. After careful study, I have concluded that C. Müller and J. Cardot described minor variations of *C. pinnata,* i.e., *Sphaerotheciella pinnata* (B.S.G.) Manuel.

2. The decision to reduce *Cryphaea corrugata* was based on a consideration of the gametophore. The lectotype lacks sporophytes and protonemata.

3. There seems to be a weak correlation between leaf areolation and the shape of the leaf apex. Leaves having acuminate apices have narrowly elliptic medial and apical cells, whereas leaves with apices somewhat abruptly contracted into wide, short acumina have elliptic to widely elliptic medial cells and narrowly elliptic to fusiform apical cells. A few exceptions to this correlation, i.e., intermediates, are known.

4. Bartram's (1949) report of *Cryphaea pinnata* from Guatemala was based on misdeterminations.

SPECIMENS EXAMINED. **Mexico. Hidalgo:** near Pellillos along Hwy 85, ca 24 mi S of Jacala, *Norris 17054* (MANUEL). Near Honey Station, *Pringle 10490* (FH,TENN), *15047* (FH). Above Real del Monte, 9400 ft, *Sharp 519* (NY). Below Las Ventanas near Mineral el Chico, 3100 m, *Sharp et al. 1687* (MANUEL). Jacala, *Sharp,* 17 Dec. 1962 (TENN). **Oaxaca:** Llano de Las Flores, N of Oaxaca, 2000–2500 m, *Iwatsuki & Sharp 5264–b* (TENN). Cerro do San Felípe on Hwy 175 through Sierra Juárez, 2500 m, *Sharp et al. 2358* (MANUEL). **Puebla:** Chinantla, *Liebmann 49* (BM), *Liebmann 8110* (CO), *Liebmann s.n.* (H–BR). **San Luis Potosí:** along Hwy 70, 23 mi E of San Luis Potosí, near k–226, 7600 ft, *Magill 2582* (TENN). Alvarez, *Orcutt 6523* (FH). **Veracruz:** El Puerto, 7600 ft, *Crum 581b* (TENN). Santa Rita, *Sharp et al. 3016a* (TENN). Atzalan, 5700 ft, *Sharp 5581* (MANUEL). Without locality. *Liebmann s.n.* (BM). **Venezuela. Merida:** Mucurubá, 2600 m, *Gehriger 280* (FH–Bart.).

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